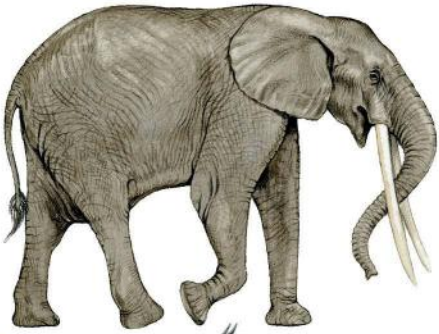
THE KINGDON FIELD GUIDE TO AFRICAN MAMMALS

SECOND EDITION



JONATHAN KINGDON

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About the author

Jonathan Kingdon was born in Tanganyika and has spent the better part of his life in Africa. He taught at Makerere University, Kampala, for many years and is now a Research Associate at the Department of Zoology, University of Oxford. He has been acclaimed as both a leading academic and a prominent artist, and awarded several prizes and medals. The millennium issue of *American Scientist* named his seven-volume *East African Mammals: an Atlas of Evolution in Africa* as one of the 'One Hundred Books that Shaped a Century of Science'. Richard Dawkins describes him as 'a world-class zoologist, ecologist and writer…a Living World Treasure…an artist with words and a poet with images'. First published in 1997, the *Kingdon Field Guide to African Mammals* was characterised as 'a work of almost heroic proportions…an extraordinary fusion between science, natural history and art' (Tim Flannery). The second edition of this guide greatly augments that work, incorporating much information accumulated over the intervening years. Kingdon was also founder and senior editor of the six-volume *Mammals of Africa*, which was awarded the prestigious Dartmouth Medal in 2014 by the American Library Association. Many of his 16 books (totalling 5,000 pages) have been translated into languages other than English and he has published numerous papers, articles and chapters. Exhibitions of his work have been shown in museums and galleries in Africa, Australia, Europe, Asia and the USA.

CONTENTS

Preface and acknowledgements 6
Checklist of species 8
Introduction to the first edition 20
Introduction to the second edition 21
- Naming and mapping species 23
- Using this guide 27
- Finding and recording mammals 28

The African environment 30
- The past 30
- Physical landscape 33
- Climate 36
- Vegetation 37

PROFILES OF ALL MAMMAL SPECIES 45
Conservation 619
Further reading 624
Glossary 625
Index 632

PREFACE AND ACKNOWLEDGEMENTS

The motivation and impetus to prepare a guide to the African continent's greatest natural resource, its mammals, came from a mix of immediate and more distant influences. My parents, my ayah, Saidi Batale, and naturalists such as Bill Moore-Gilbert, Hamisi Sikana, Willoughby Lowe, Mtemi Senge Masembe, Hugh Elliot and Fairfax Bell illuminated a nomadic youth in Tanganyika. As a child I was subject to the vulnerabilities of existence during war-time, and a witness to famine, floods, locust swarms and grand dramas of life and death on the plains of Serengeti. I learned, early on, that all the glories of animal and plant life that surrounded me were no less than life's parade of triumph over all the vicissitudes that being and time could throw at them. My childhood awe for nature's dangerous beauty and wasteful fecundity soon led on to a more disciplined interest in natural history and an explicitly Darwinian outlook on life. Reg Moreau and Desmond Vesey-FitzGerald were early influences while L.S.B. Leakey, Sir Julian Huxley, Peter Miller, Leonard Beadle and Alan Walker were among those who helped, and provoked, my compiling *East African Mammals: An Atlas of Evolution in Africa* (Kingdon 1971-82). That work was an essential precursor to this book; indeed, since its publication there has been continuous pressure, from friends and publishers alike, to condense the text and enlarge the range of that work to embrace a continental scope. That, in turn, led on to the *Mammals of Africa* project, which was published in six volumes in 2013. I owe gratitude to all my fellow authors and editors on *Mammals of Africa*, most especially my brilliant co-editor, Mike Hoffmann.

A decisive influence on this field guide came from my family, especially my sons: Zachary, who read, processed, discussed and helped refine the entire text of the first edition, and Rungwe, who firmly pushed me into taking the first plunge. Elena selflessly supported a lifetime of research on mammals. This second edition owes its existence and completion to Laura.

I am indebted to many institutions for their support over the years, from Makerere University in Uganda, WildCRU at Oxford University in England, CSIRO in Australia, Skidmore College and Duke University in the United States to briefer or less formal associations with Kyoto University, Japan, various museums both within and outside Africa, Wildlife Departments, National Parks and numerous universities. I owe some independence of mind and movement to all those who have purchased my paintings, drawings, prints, sculptures and books.

The contents of this field guide are drawn from observations made in various parts of Africa, often in the company of friends and colleagues. They are also compiled from publications, correspondence and conversation with more people than can be acknowledged by name but some have had a more direct role. Tim Davenport, Morris Gosling, Colin Groves, David Pye, Simon Bearder, Alan Root, Joan Root, David Macdonald, Claudio Sillero, Patrick Duncan, Mark Stanley Price, Redmond O'Hanlon, Tom Butynski, Annie Gautier, Hilary Morland and John Fanshawe vetted structure, blocks of text or illustrations for the first edition. Annie and Jean-Pierre Gautier, Tom Butynski, Steve Gartlan and many others, including Tony Archer, John Skinner, Chris Hillman, Andrew Conroy, Gerard and Ahn Galat, Leslie Scott, Doug Shiel, Caroline Tutin, Tom Struhsaker, Lysa Leland, Robert Glen, Dick Estes, Keith Eltringham, Russel Friedman, Margaret Kinnaird, Tim O'Brien, Fritz Vollrath and Tim Davenport have hosted me in camps or homes in Africa. Their company, ideas and hospitality have contributed in more ways than can begin to be enumerated. Likewise wildlife and national park authorities in many African countries (notably Tanzania, Kenya, Uganda, Ethiopia, Côte d'Ivoire and Cameroon) have helped with permits, hospitality, transport and guidance, assistance that has been vital in building up a broad overview as well as detailed documentation of the mammals. The Wellcome Trust gave vital aid (1968–78).

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Perhaps this short list of today's enthusiasts will help give heart to tomorrow's warriors, who must carry on the fight to save Africa's fauna and flora and the deeper realities of which they are an expression.

CHECKLIST OF SPECIES

MAMMALIA MAMMALS 45

AFROTHERES AFROTHERIA 48

Paenungulata 48

HYRAXES HYRACOIDEA 49

Hyraxes Procaviidae 50
- Rock hyraxes *Procavia* 51
- Bush Hyrax *Heterohyrax brucei* 52

Tree hyraxes *Dendrohyrax* 53
- Eastern Tree Hyrax *Dendrohyrax validus* 53
- Southern Tree Hyrax *Dendrohyrax arboreus* 54
- Western Tree Hyrax *Dendrohyrax dorsalis* 55

PROBOSCIDS PROBOSCIDEA 56

Elephants Elephantidae 57
- Forest Elephant *Loxodonta cyclotis* 58
- Bush Elephant *Loxodonta africana* 59

SEA-COWS SIRENIA 64

Dugong Dugongidae 64
- Dugong *Dugong dugon* 64

Manatees Trichechidae 66
- West African Manatee *Trichechus senegalensis* 67

Afroinsectiphillia 68

AFROSORICIDS AFROSORICIDA 68

Otter-shrews Tenrecidae, Potamogalinae 69
- Giant Otter-shrew *Potamogale velox* 69
- Mount Nimba Otter-shrew *Micropotamogale lamottei* 69
- Rwenzori Otter-shrew *Mesopotamogale ruwenzorii* 70

Golden-moles Chrysochloridae 70
- Giant golden-moles *Chrysospalax* 71
- Yellow golden-moles *Calcochloris* 71
- Desert Golden-mole *Eremitalpa granti* 73
- Cryptic golden-moles *Cryptochloris* 74
- Stuhlmann's Golden-mole *Kilimatalpa stuhlmanni* 74
- Cape golden-moles *Chrysochloris* 74
- Congo Golden-mole *Huetia leucorhinus* 74
- Forty-toothed golden-moles *Chlorotalpa* 75
- Arends's Golden-mole *Carpitalpa arendsi* 75
- Lesser narrow-headed golden-moles *Neamblysomus* 75
- Narrow-headed golden-moles *Amblysomus* 75

SENGIS (ELEPHANT-SHREWS) MACROSCELIDEA 76

Soft-furred sengis (Soft-furred elephant-shrews) Macroscelidinae 76
- Four-toed Sengi *Petrodromus tetradactylus* 77
- Round-eared Sengi *Macroscelides proboscideus* 78
- Lesser sengis *Elephantulus* 78

Giant sengis (Giant elephant-shrews) Rhynchocyoninae 80

Giant sengis *Rhynchocyon* 81
- Udzungwa Giant Sengi *Rhynchocyon udzungwensis* 81
- Mandela's Giant Sengi *Rhynchocyon* sp. nov. 81
- Golden-rumped Giant Sengi *Rhynchocyon chrysopygus* 84
- Black-and-rufous Giant Sengi *Rhynchocyon petersi* 84
- Chequered Giant Sengi *Rhynchocyon cirnei* 85

AARDVARK TUBULIDENTATA 86

Aardvark Orycteropodidae 86
- Aardvark *Orycteropus afer* 86

PRIMATES PRIMATES 89

Old World monkeys, apes and humans Catarrhini 90
Apes and humans Hominidae 90

Gorillas *Gorilla* 91
- Western Gorilla *Gorilla gorilla* 91
- Eastern Gorilla *Gorilla beringei* 93

Chimpanzees *Pan* 95
- Common Chimpanzee *Pan troglodytes* 95
- Bonobo (Gracile Chimpanzee) *Pan paniscus* 97

Hominins Hominini 99

Old World monkeys Cercopithecoidea: Cercopithecidae 100

Colobus monkeys Colobinae 101
- Olive Colobus *Procolobus verus* 102

Red colobus monkeys *Piliocolobus* 103
- Zanzibar Red Colobus *Piliocolobus kirkii* 105
- Udzungwa Red Colobus *Piliocolobus gordonorum* 105
- Tana River Red Colobus *Piliocolobus rufomitratus* 106
- Tshuapa Red Colobus *Piliocolobus tholloni* 107
- Central African Red Colobus *Piliocolobus oustaleti* 107
- Pennant's Red Colobus *Piliocolobus pennantii* 108
- Niger Delta Red Colobus *Piliocolobus epieni* 109
- Preuss's Red Colobus *Piliocolobus preussi* 109
- Waldron's Red Colobus *Piliocolobus waldronae* 110
- Western Red Colobus *Piliocolobus badius* 110

Pied (black-and-white) colobus monkeys *Colobus* 111
- Black Colobus *Colobus satanus* 111
- King Colobus *Colobus polykomos* 112
- Angola Colobus *Colobus angolensis* 112
- Geoffroy's Colobus *Colobus vellerosus* 114
- Guereza Colobus *Colobus guereza* (syn. *C. abyssinicus*) 114

Cheek-pouched monkeys Cercopithecinae 116

Baboons *Papio* 117
- Sacred Baboon *Papio hamadryas* 118
- Guinea Baboon *Papio papio* 119
- Olive Baboon *Papio anubis* 120
- Yellow Baboon *Papio cynocephalus* 121
- Chacma Baboon *Papio ursinus* 121

Kipunji *Rungwecebus* 122
- Kipunji *Rungwecebus kipunji* 123

Baboon-mangabeys *Lophocebus* 124
- Grey-cheeked Mangabey *Lophocebus albigena* 125
- Black Mangabey *Lophocebus aterrimus* 126

Gelada *Theropithecus* 127
- Gelada *Theropithecus gelada* 127

Mandrills *Mandrillus* 129
- Mandrill *Mandrillus sphinx* 129
- Drill *Mandrillus leucophaeus* 130

Drill-mangabeys *Cercocebus* 132
- Golden-bellied Mangabey *Cercocebus chrysogaster* 133
- Red-capped Mangabey *Cercocebus torquatus* 134
- White-naped Mangabey *Cercocebus lunulatus* 134
- Sooty Mangabey *Cercocebus atys* 135
- Agile Mangabey *Cercocebus agilis* 136
- Tana River Mangabey *Cercocebus galeritus* 136
- Sanje Mangabey *Cercocebus sanjei* 137

Macaques *Macaca* 138
- Barbary Macaque *Macaca sylvanus* 138

Guenons and allies Cercopithecini 139

Swamp monkey *Allenopithecus* 143
- Allen's Swamp Monkey *Allenopithecus nigroviridis* 143

Talapoins *Miopithecus* 145
- Northern Talapoin *Miopithecus ogouensis* 145
- Southern Talapoin *Miopithecus talapoin* 146

Patas monkey *Erythrocebus* 147
- Patas Monkey *Erythrocebus patas* 147

Savanna monkeys *Chlorocebus* group 148
- Grivet Monkey *Chlorocebus aethiops* 150
- Tantalus Monkey *Chlorocebus tantalus* 151
- Vervet Monkey *Chlorocebus pygerythrus* 151
- Green Monkey *Chlorocebus sabaeus* 152
- Bale Monkey *Chlorocebus djamdjamensis* 152

Mountain monkeys *Allochrocebus* group 154
- L'Hoest's Monkey *Allochrocebus lhoesti* 155
- Preuss's Monkey *Allochrocebus preussi* 156
- Sun-tailed Monkey *Allochrocebus solatus* 157

Arboreal guenons *Cercopithecus* 158

Dryad monkeys *Cercopithecus (dryas)* group 158
- Dryad Monkey *Cercopithecus (dryas) dryas* 158
- Salongo Monkey *Cercopithecus (dryas) salongo* 159

Diana monkeys *Cercopithecus (diana)* group 159
- Diana Monkey *Cercopithecus (diana) diana* 159
- Roloway Monkey *Cercopithecus (diana) roloway* 160
- De Brazza's Monkey *Cercopithecus neglectus* 161

Mona monkeys *Cercopithecus (mona)* group 163
- Mona Monkey *Cercopithecus (mona) mona* 164
- Campbell's Monkey *Cercopithecus (mona) campbelli* 165
- Lowe's Monkey *Cercopithecus (mona) lowei* 165
- Dent's Monkey *Cercopithecus (mona) denti* 166
- Wolf's Monkey *Cercopithecus (mona) wolfi* 167
- Crowned Monkey *Cercopithecus (mona) pogonias* 168

Long-faced monkeys *Cercopithecus (hamlyni)* group 169
- Owl-faced Monkey *Cercopithecus (hamlyni) hamlyni* 170
- Lesula Monkey *Cercopithecus (hamlyni) lomamiensis* 171

Gentle monkeys *Cercopithecus (nictitans)* group 172
- Putty-nosed Monkey *Cercopithecus (nictitans) nictitans* 174
- Gentle Monkey *Cercopithecus (nictitans) mitis* 175

Cephus monkeys *Cercopithecus (cephus)* group 177
- Lesser Spot-nosed Monkey *Cercopithecus (cephus) petaurista* 179
- White-throated Monkey *Cercopithecus (cephus) erythrogaster* 179
- Sclater's Monkey *Cercopithecus (cephus) sclateri* 180
- Moustached Monkey *Cercopithecus (cephus) cephus* 181
- Red-eared Monkey *Cercopithecus (cephus) erythrotis* 182
- Red-tailed Monkey *Cercopithecus (cephus) ascanius* 183

PROSIMIANS STREPSIRRHINI 185

Lorisids Lorisidae 186
- Common Potto *Perodicticus potto* 186
- Martin's Potto *Pseudopotto martini* 188

Angwantibos *Arctocebus* 188
- Calabar Angwantibo *Arctocebus calabarensis* 188

- Golden Angwantibo *Arctocebus aureus* 189

Galagos or bushbabies Galagidae 190

Dwarf galagos *Galagoides* 194

Crescendo callers (Equatorial dwarf galagos) 194
- Demidoff's Galago *Galagoides demidoff* 195
- Thomas's Galago *Galagoides thomasi* 195

Scaling caller (Montane dwarf galago) 197
- Usambara Galago *Galagoides orinus* 197

Incremental callers (East coast dwarf galagos) 197
- Mozambique Galago *Galagoides granti* 198
- Diani Galago *Galagoides cocos* 198

Roller callers (East coast dwarf galagos) 199
- Rondo Galago *Galagoides rondoensis* 199
- Zanzibar Galago *Galagoides zanzibaricus* 200

Squirrel galagos *Sciurocheirus* 201
- Allen's Squirrel Galago *Sciurocheirus alleni* 201
- Gabon Squirrel Galago *Sciurocheirus gabonensis* 202
- Makandé Squirrel Galago *Sciurocheirus makandensis* 202

Greater galagos *Otolemur* 203
- Greater Galago *Otolemur crassicaudatus* 204
- Small-eared Galago *Otolemur garnettii* 205

Needle-clawed galagos *Euoticus* 206
- Elegant Galago *Euoticus elegantulus* 207
- Pallid Galago *Euoticus pallidus* 207

Lesser galagos *Galago* 208
- Spectacled Galago *Galago matschiei* (syn. *G. inustus*) 209
- Senegal Galago *Galago senegalensis* 210
- Southern Galago *Galago moholi* 210
- Somali Galago *Galago gallarum* 211

RODENTS RODENTIA 212

Hystricomorpha (Ctenohystrica)

Gundis Ctenodactylidae 214
- Gundis *Ctenodactylus* 214
- Pectinator *Pectinator spekei* 215
- Senegal Gundi *Felovia vae* 215
- Fringe-eared Gundi *Massouteria mzabi* 216

Porcupines Hystricidae 216
- Brush-tailed Porcupine *Atherurus africanus* 217
- Crested Porcupine *Hystrix cristata* 217
- South African Porcupine *Hystrix africaeaustralis* 218

Cane rats Thryonomyidae 219
- Savanna Cane Rat *Thryonomys gregorianus* 219
- Marsh Cane Rat *Thryonomys swinderianus* 220

Noki (Dassie Rat) Petromuridae 220
- Noki (Dassie Rat) *Petromus typicus* 220

Blesmols Bathyergidae 221
- Silky Blesmol (Silvery Mole-rat) *Heliophobius argenteocinereus* 221
- Dune blesmols (Dune mole-rats) *Bathyergus* 222
- Cape Blesmol *Georychus capensis* 222
- Common blesmols *Cryptomys* 223

Sand-puppy Heterocephalidae 224
- Sand-puppy (Naked Mole-rat) *Heterocephalus glaber* 224

Sciuromorpha

Squirrels Sciuridae 225

Sun squirrels *Heliosciurus* 225
- Rwenzori Sun Squirrel *Heliosciurus ruwenzori* 225
- Zanj Sun Squirrel *Heliosciurus undulatus* 226
- Mutable Sun Squirrel *Heliosciurus mutabilis* 226
- Red-legged Sun Squirrel *Heliosciurus rufobrachium* 227

- Gambian Sun Squirrel *Heliosciurus gambianus* 227
- Punctate Sun Squirrel *Heliosciurus punctatus* 228

- African Pygmy Squirrel *Myosciurus pumilio* 228

- African Giant Squirrel *Protoxerus stangeri* 229
- Slender-tailed Squirrel *Allosciurus aubinnii* 229

Palm squirrels *Epixerus* 230
- Western Palm Squirrel *Epixerus ebii* 230
- Biafran Bight Palm Squirrel *Epixerus wilsoni* 230

Rope squirrels *Funisciurus* 231
- Carruthers's Mountain Squirrel *Funisciurus carruthersi* 231
- Ribboned Rope Squirrel *Funisciurus lemniscatus* 232
- Lunda Rope Squirrel *Funisciurus bayonii* 232
- Thomas's Rope Squirrel *Funisciurus anerythrus* 233
- Red-cheeked Rope Squirrel *Funisciurus leucogenys* 233
- Fire-footed Rope Squirrel *Funisciurus pyrropus* 234
- Kintampo Rope Squirrel *Funisciurus substriatus* 234
- Du Chaillu's Rope Squirrel *Funisciurus duchaillui* 235
- Lady Burton's Rope Squirrel *Funisciurus isabella* 235
- Congo Rope Squirrel *Funisciurus congicus* 236

Bush squirrels *Paraxerus* 236
- Alexander's Bush Squirrel *Paraxerus alexandri* 237
- Cooper's Mountain Squirrel *Paraxerus cooperi* 237
- Green Bush Squirrel *Paraxerus poensis* 238
- Böhm's Bush Squirrel *Paraxerus boehmi* 238
- Striped Bush Squirrel *Paraxerus flavovittis* 239
- Ochre Bush Squirrel *Paraxerus ochraceus* 239
- Smith's Bush Squirrel *Paraxerus cepapi* 240

Tanganyika mountain squirrels *Paraxerus (lucifer)* group 240
- Red Tanganyika Mountain Squirrel *Paraxerus (lucifer) lucifer* 240
- Kipengere Mountain Squirrel *Paraxerus (lucifer) laetus* 241
- Kilimanjaro Mountain Squirrel *Paraxerus (lucifer) byatti* 241
- Lushoto Mountain Squirrel *Paraxerus (lucifer) vexillarius* 241

- Vincent's Bush Squirrel *Paraxerus vincenti* 242
- Red-bellied Bush Squirrel *Paraxerus palliatus* 242

Ground squirrels *Xerus* 243
- Striped Ground Squirrel *Xerus erythropus* 243
- Damara Ground Squirrel *Xerus princeps* 243
- South African Ground Squirrel *Xerus inauris* 244
- Unstriped Ground Squirrel *Xerus rutilus* 245
- Barbary Ground Squirrel *Xerus* (previously *Atlantoxerus*) *getulus* 245

Dormice Gliridae (formerly Myoxidae) 246

African dormice *Graphiurus* 246
- West African Smoky Dormouse *Graphiurus (Aethoglis) nagtaglasi* 246
- Small-eared dormice *Graphiurus (Claviglis)* 247
- African rock dormice *Graphiurus (Gliriscus)* 247
- African dormice *Graphiurus (Graphiurus)* 248

- Orchard dormice *Eliomys* 249

Anomaluromorpha
Anomalures Anomaluridae 249
- Lord Derby's Anomalure *Anomalurus derbianus* 251
- Pel's Anomalure *Anomalurus peli* 252
- Lesser Anomalure *Anomalurus pusillus* 252
- Beecroft's Anomalure *Anomalurus beecrofti* 253
- Zenker's Flying Mouse *Idiurus zenkeri* 254
- Long-eared Flying Mouse *Idiurus macrotis* 254
- Cameroon Scaly-tail *Zenkerella insignis* 255

Springhares Pedetidae 255
- Springhares *Pedetes* 256

Myomorpha (embracing Muroidea and Dipodidae) 257
Jerboas Dipodidae 257
- Four-toed Jerboa *Allactaga tetradactyla* 257
- Desert jerboas *Jaculus* 258

Mole-rats and root-rats Spalacidae 259
- Palestine Mole-rat *Spalax ehrenbergi* 259
- Root-rats *Tachyoryctes* 259

Archaic muroids Nesomyidae 260
- Delaney's Mouse *Delanymys brooksi* 261
- Pygmy rock mice *Petromyscus* 261
- White-tailed Mouse *Mystromys albicaudatus* 262

Pouched rats Cricetomyine nesomyids 262
- Lesser Pouched Rat *Beamys hindei* 262
- Giant pouched rats *Cricetomys* 263
- Pouched mice *Saccostomus* 263
- Fat mice *Steatomys* 264
- Large-eared Mouse *Malacothrix typica* 264

Climbing mice 'Dendromurine' nesomyids 264
- Bates's Climbing Mouse *Prionomys batesi* 265
- Velvet Climbing Mouse *Dendroprionomys rousseloti* 265
- African climbing mice *Dendromus* 265
- Giant Climbing Mouse *Megadendromus nicolausi* 266

Cricetid muroids Cricetidae 267
- Mediterranean Vole *Microtus guentheri* 267

Murids Muridae 268
Crested (Maned) Rat Lophiomyinae 268
- Crested (Maned) Rat *Lophiomys imhausi* 270

Hair-modified rats Deomyinae 271
- Uranomys Mouse *Uranomys ruddi* 271
- Link Rat *Deomys ferugineus* 271
- Brush-furred mice *Lophuromys* 272
- Spiny mice *Acomys* 272

Togo Mouse Leimacomyinae 273
- Togo Mouse *Leimacomys buettneri* 273

Gerbils Gerbillinae 274
- Fat-tailed Gerbil *Pachyuromys duprasi* 274
- Brauer's Dwarf Gerbil *Desmodilliscus braueri* 275
- Namaqua Gerbil *Desmodillus auricularis* 275
- Slender gerbils (taterils) *Taterillus* 275
- Sand rats *Psammomys* 276
- Jirds *Meriones* 277
- Bushy-tailed Jird *Sekeetamys calurus* 277
- Gerbils *Gerbillus* 278
- Peel's Pygmy Gerbil *Microdillus peeli* 278
- Walo (Ammodile) *Ammodillus imbellis* 279
- Robust gerbils *Gerbilliscus* (formerly *Tatera*) 279
- Hairy-footed gerbils *Gerbillurus* 280

Rats and mice Murinae 280

Recent immigrant murines and descendents 281
- Black Rat *Rattus rattus* 281
- Short-tailed Bandicoot Rat *Nesokia indica* 281
- Long-tailed Field Mouse *Apodemus sylvaticus* 282
- Common mice *Mus* 282
- Wurch Mouse *Muriculus imberbis* 283

African omnivorous murines (omni-murines) 284
- Meadow mice *Myomyscus* (*'Myomys'*) 285
- Soft-furred rats *Praomys* 285
- Long-footed rats (swamp rats) *Malacomys* 286
- Velvet rats *Colomys* 286
- Broad-headed stink rats *Zelotomys* 287
- Multimammate rats *Mastomys* 287
- Ethiopian meadow rats *Stenocephalemys* 288
- De Balsac's Mouse *Heimyscus fumosus* 288
- African wood mice *Hylomyscus* 289

African herbivorous murines (herbi-murines) 289

African herbivorous murines (south-east lineage: Otomyini) 290
- Whistling rats *Parotomys* 290
- Cape ice rats *Myotomys* (formerly *Liotomys*) 291
- Groove-toothed rats *Otomys* 291

African herbivorous murines (mainstream herbi-murines) 292
- Rusty-nosed rats *Oenomys* 293
- Mount Oku Rat *Lamottemys okuensis* 293
- Broad-footed thicket rats *Thamnomys* 294
- Hump-nosed mice *Hybomys* group 294
- Defua Rat *Dephomys defua* 295
- Target Rat *Stochomys longicaudatus* 295
- Bush rats *Aethomys* 295
- Namaqua rock mice *Micaelamys* 296
- Acacia rats *Thallomys* 297
- Narrow-footed thicket rats *Grammomys* 297
- Shaggy swamp rats *Dasymys* 298
- Four-striped Grass Mouse *Rhabdomys pumilio* 299
- Dega rats *Desmomys* 299
- Creek rats *Pelomys* 300
- Mill rats *Mylomys* 300
- Zebra mice *Lemniscomys* 301
- Grass rats *Arvicanthis* 302

HARES, ROCK-HARES AND RABBITS LAGOMORPHA 303

Hares, rock-hares and rabbits Leporidae 304
- Bunyoro Rabbit *Poelagus marjorita* 304

Rock-hares *Pronolagus* 304
- Smith's Red Rock-hare *Pronolagus rupestris* 305
- Hewitt's Red Rock-hare *Pronolagus saundersiae* 305
- Natal Red Rock-hare *Pronolagus crassicaudatus* 306
- Jameson's Red Rock-hare *Pronolagus randensis* 306
- Common Rabbit *Oryctolagus cuniculus* 307
- Riverine Rabbit *Bunolagus monticularis* 307

True hares *Lepus* 308
- Cape Hare *Lepus capensis* (includes *L. fagani* and *L. habessinicus*) 309
- Scrub Hare *Lepus saxatilis* (includes *L. victoriae* and *L. crawshayi*) 309
- Starck's Hare *Lepus starcki* 310

HEDGEHOGS ERINACEOMORPHA 311

Hedgehogs Erinaceidae 311
- African hedgehogs *Atelerix* 311
- Long-eared Hedgehog *Hemiechinus auritus* 312
- Desert Hedgehog *Paraechinus aethiopicus* 313

SHREWS SORICOMORPHA 314

Shrews Soricidae 314
- Mouse shrews *Myosorex* 315
- Mole shrews *Surdisorex* 315
- Congo shrews *Congosorex* 316
- Musk shrews *Suncus* 316
- Forest shrews *Sylvisorex* 317
- Hero shrews *Scutisorex* 317
- Rwenzori Water Shrew *Ruwenzorisorex suncoides* 318
- Rodent shrews *Paracrocidura* 319
- White-toothed shrews *Crocidura* 319

BATS CHIROPTERA 322

Fruit bats Pteropodidae 325
- Flying-foxes *Pteropus* 327
- Straw-coloured Fruit Bat *Eidolon helvum* 328
- Tear-drop Fruit Bat *Scotonycteris zenkeri* 328
- Golden fruit bats *Casinycteris* 329
- Egyptian Rousette *Rousettus aegyptiacus* 329
- Mountain Fruit Bat *Stenonycteris lanosus* 330
- Angola Fruit Bat *Lissonycteris angolensis* 330
- Collared fruit bats *Myonycteris* 331
- Nectar Bat *Megaloglossus woermanni* 331
- Hammer-headed Fruit Bat *Hypsignathus monstrosus* 332
- Singing fruit bats *Epomops* 333
- Benguela Fruit Bat *Plerotes anchietae* 334
- Flying Calf *Nanonycteris veldkampi* 334
- Dwarf epauletted fruit bats *Micropteropus* 335
- Epauletted fruit bats *Epomophorus* 335

Mouse-tailed bats Rhinopomatidae 337
- Mouse-tailed bats *Rhinopoma* 337

Large-winged bats Megadermatidae 337
- Heart-nosed Bat *Cardioderma cor* 338
- Yellow-winged Bat *Lavia frons* 338

Horseshoe bats Rhinolophidae 339
- Horseshoe bats *Rhinolophus* 339

Leaf-nosed bats Hipposideridae 340
- Leaf-nosed bats *Hipposideros* 340
- Trident leaf-nosed bats *Asellia* 341
- Percival's Trident Bat *Cloeotis percivali* 341
- African Leaf-nosed Bat *Triaenops afer* 342

Slit-faced bats Nycteridae 342
- Slit-faced bats *Nycteris* 343

Sheath-tailed bats Emballonuridae 344
- African Sheath-tailed Bat *Coleura afra* 344
- Tomb bats *Taphozous* 344
- Black-hawk Bat *Saccolaimus peli* 345

Free-tailed bats Molossidae 346
- Guano bats *Tadarida* 346
- Wrinkle-lipped bats *Chaerophon* 347
- Mops free-tailed bats *Mops* 347
- Winged-mouse bats *Myopterus* 348
- Flat-headed bats *Mormopterus* 348
- East African Flat-headed Bat *Platymops setiger* 348
- Roberts's Flat-headed Bat *Sauromys petrophilus* 349
- Giant Mastiff Bat *Otomops martiensseni* 349

Long-fingered bats Miniopteridae 350
- Long-fingered bats *Miniopterus* 350

Pimple-winged bats Cistugidae 351
- Pimple-winged bats *Cistugo* 351

Vesper bats Vespertilionidae 351
- Hairy bats *Myotis* 353
- Woolly bats *Kerivoula* 353
- House bats *Scotophilus* 354
- Evening bats *Scotoecus* 354
- Schlieffen's Twilight Bat *Nycticeinops schlieffeni* 355
- Long-eared bats *Plecotus* 355
- Hemprich's Long-eared Bat *Otonycteris hemprichii* 355
- Barbastelle bats *Barbastella* 356
- Butterfly bats *Glauconycteris* 356
- Badger Bat *Niumbaha superba* 357
- Tropical long-eared bats *Laephotis* 357
- Serotine bats *Eptesicus* 358
- Moloney's Flat-headed Bat *Mimetillus moloneyi* 358
- Noctules *Nyctalus* 359
- Pipistrelles *Pipistrellus* 359

CARNIVORES CARNIVORA 360

Dogs and allies Caniformia 363
Dogs and allies Canidae 363

Wild Dog, jackals and wolves *Canis* 365
- African Wild Dog *Canis pictus* 365
- Side-striped Jackal *Canis adustus* 367

- Black-backed Jackal *Canis mesomelas* 368
- Ethiopian Wolf *Canis simensis* 369
- Common Jackal *Canis aureus* 370
- Grey Wolf *Canis lupus* 371

- Bat-eared Fox *Otocyon megalotis* 372

Foxes *Vulpes* 373
- Royal Fox *Vulpes cana* 373
- Fennec Fox *Vulpes zerda* 373
- Cape Fox *Vulpes chama* 374
- Pale Fox *Vulpes pallida* 375
- Rüppell's Fox *Vulpes rueppelli* 375
- Red Fox *Vulpes vulpes* 376

Mustelids Mustelidae 377
- Ratel *Mellivora capensis* 378

Weasels and polecats *Mustela* 380
- Common Weasel *Mustela nivalis* 380
- Polecat *Mustela putorius* 380

- Libyan Striped Weasel *Poecilictis libyca* 381
- Zorilla *Ictonyx striatus* 381
- African Striped Weasel *Poecilogale albinucha* 382

Otters Lutrinae 383
- Spotted-necked Otter *Hydrictis maculicollis* 384
- Common Otter *Lutra lutra* 385
- Congo Clawless Otter *Aonyx congicus* 386
- African Clawless Otter *Aonyx capensis* 387

Seals Pinnipedia 388
Fur seals Otariidae 388

Fur seals *Arctocephalus* 388
- Cape Fur Seal *Arctocephalus pusillus* 388

True seals Phocidae 389

Monk seals *Monachus* 390
- Mediterranean Monk Seal *Monachus monachus* 390

Cats and allies Feliformia 391
Tree Civet Nandiniidae 391
- Tree Civet *Nandinia binotata* 391

Cats Felidae 393
- Lion *Panthera leo* 394
- Leopard *Panthera pardus* 397
- Serval *Leptailurus serval* 398
- African Golden Cat *Profelis aurata* 400
- Caracal *Caracal caracal* 401
- Cheetah *Acinonyx jubatus* 403
- Swamp Cat *Felis chaus* 405
- Wildcat *Felis sylvestris* 405
- Black-footed Cat *Felis nigripes* 406
- Sand Cat *Felis margarita* 407

Genets and civets Viverridae 408
- African Civet *Civettictis civetta* 409

Oyans *Poiana* 410
- Central African Oyan *Poiana richardsoni* 410
- West African Oyan *Poiana leightoni* 411

Genets *Genetta* 412
- Ethiopian Genet *Genetta abyssinica* 412
- Hausa Genet *Genetta thierryi* 413
- Giant Genet *Genetta victoriae* 413
- Servaline Genet *Genetta servalina* 414
- Crested Genet *Genetta cristata* 414
- Johnston's Genet *Genetta johnstoni* 415
- Aquatic Genet *Genetta* (formerly *Osbornictis*) *piscivora* 415
- Common Genet *Genetta genetta* 416
- Feline Genet *Genetta felina* 417
- Miombo Genet *Genetta angolensis* 418
- Cape Genet *Genetta tigrina* 418
- Blotched Genet *Genetta maculata* 419
- Pardine Genet *Genetta pardina* 419
- King Genet *Genetta poensis* 420
- Bourlon's Genet *Genetta bourloni* 421

Hyaenids Hyaenidae 421
- Striped Hyaena *Hyaena hyaena* 423
- Brown Hyaena *Hyaena brunnea* 424
- Spotted Hyaena *Crocuta crocuta* 426

Aardwolf Protelinae 428
- Aardwolf *Proteles cristata* 428

Mongooses Herpestidae 430

Solitary mongooses Herpestinae 432
- Long-snouted Mongoose *Xenogale naso* 432
- Marsh Mongoose *Atilax paludinosus* 433

Common mongooses *Herpestes* 434
- Ichneumon Mongoose *Herpestes ichneumon* 434
- Slender Mongoose *Herpestes sanguineus* 435
- Angola Slender Mongoose *Herpestes flavescens* 436
- Small Grey Mongoose *Herpestes pulverulenta* 436
- Somali Slender Mongoose *Herpestes ochraceus* 437
- Yellow Mongoose *Cynictis penicillata* 437
- Selous's Mongoose *Paracynictis* (formerly *Cynictis*) *selousi* 438
- White-tailed Mongoose *Ichneumia albicauda* 439
- Meller's Mongoose *Rhynchogale melleri* 440

Four-toed or dog mongooses *Bdeogale* 441
- Bushy-tailed Mongoose *Bdeogale crassicauda* 442
- Sokoke Dog Mongoose *Bdeogale omnivora* 442
- Black-legged Mongoose *Bdeogale nigripes* 443
- Jackson's Mongoose *Bdeogale jacksoni* 444

Social mongooses Mungotinae 444
- Meerkat *Suricata suricata* 445
- Banded Mongoose *Mungos mungo* 446
- Gambian Mongoose *Mungos gambianus* 448
- Liberian Mongoose *Liberiictis kuhni* 448

Cusimanses *Crossarchus* 449
- Ansorge's Cusimanse *Crossarchus ansorgei* 450
- Common Cusimanse *Crossarchus obscurus* 450
- Cameroon Cusimanse *Crossarchus platycephalus* 451
- Alexander's Cusimanse *Crossarchus alexandri* 451
- Savanna Mongoose *Dologale dybowski* 452
- Somali Dwarf Mongoose *Helogale hirtula* 453
- Dwarf Mongoose *Helogale parvula* 453

PANGOLINS PHOLIDOTA 455

Pangolins Manidae 455
- Long-tailed Pangolin *Uromanis tetradactyla* 456
- Tree Pangolin *Phataginus tricuspis* 457
- Giant Pangolin *Smutsia gigantea* 458
- Ground Pangolin *Smutsia temminckii* 459

ODD-TOED UNGULATES PERISSODACTYLA 461

Horses Equidae 461

African horses *Equus* 462
- Grevy's Zebra *Equus grevyi* 463
- Common Zebra *Equus quagga* 465
- Mountain Zebra *Equus zebra* 467
- African Wild Ass *Equus africanus* 469

Rhinoceroses Rhinocerotidae 470
- Black Rhinoceros *Diceros bicornis* 471
- White Rhinoceros *Ceratotherium simum* 473

EVEN-TOED UNGULATES CETARTIODACTYLA 475

Pigs Suidae 476
- Wild Boar *Sus scrofa* 477
- Bushpig *Potamochoerus larvatus* 478
- Red River Hog *Potamochoerus porcus* 479
- Giant Forest Hog *Hylochoerus meinertzhageni* 480

Warthogs *Phacochoerus* 482
- Desert Warthog *Phacochoerus aethiopicus* 483
- Common Warthog *Phacochoerus africanus* 484

Whippomorpha 486
Hippopotamuses Hippopotamidae 486
- Common Hippopotamus *Hippopotamus amphibius* 487
- Pygmy Hippopotamus *Choeropsis liberiensis* 489

Ruminants Ruminantia 490
Chevrotains Tragulidae 490
- Water Chevrotain *Hyemoschus aquaticus* 490

Giraffes Giraffidae 492
- Giraffe *Giraffa (camelopardalis)* 492
- Okapi *Okapia johnstoni* 497

Deer Cervidae 499
- Red Deer *Cervus elaphus* 499

Bovids, horned ungulates Bovidae 500

Bovines Bovinae 502

Oxen Bovini 502
- African Buffalo *Syncerus caffer* 503

Spiral-horned bovines Tragelaphini 505
- Lesser Kudu *Tragelaphus imberbis* 507
- Nyala *Tragelaphus angasi* 508
- Mountain Nyala *Tragelaphus buxtoni* 510
- Greater Kudu *Tragelaphus strepsiceros* 511
- Bushbuck *Tragelaphus scriptus* 513
- Sitatunga *Tragelaphus spekii* 515
- Bongo *Tragelaphus eurycerus* 517
- Giant Eland *Taurotragus derbianus* 518
- Common Eland *Taurotragus oryx* 519

Antelopes, sheep and goats Antilopinae 522

Dwarf antelopes Neotragini 524
- Royal Antelope *Neotragus pygmaeus* 524
- Dwarf Antelope *Neotragus batesi* 525
- Suni *Nesotragus moschatus* 526

Duikers Cephalophini 527

Blue duikers *Philantomba* 529
- Blue Duiker *Philantomba monticola* 530
- Maxwell's Duiker *Philantomba maxwelli* 531
- Walter's Duiker *Philantomba walteri* 531

- Bush Duiker *Sylvicapra grimmia* 532

Forest duikers *Cephalophus* 533
- Zebra Duiker *Cephalophus zebra* 535
- Aders's Duiker *Cephalophus adersi* 536
- Rwenzori Red Duiker *Cephalophus rubidus* 537
- White-bellied Duiker *Cephalophus leucogaster* 537
- Natal Red Duiker *Cephalophus natalensis* 538
- Harvey's Duiker *Cephalophus harveyi* 538
- Red-flanked Duiker *Cephalophus rufilatus* 539
- Black-fronted Duiker *Cephalophus nigrifrons* 540
- Ogilby's Duiker *Cephalophus ogilbyi* 540
- Weyns's Duiker *Cephalophus weynsi* 541
- Peters's Duiker *Cephalophus callipygus* 542
- Black Duiker *Cephalophus niger* 543
- Abbott's Duiker *Cephalophus spadix* 543
- Yellow-backed Duiker *Cephalophus silvicultor* 544
- Bay Duiker *Cephalophus dorsalis* 545
- Jentink's Duiker *Cephalophus jentinki* 546

Grysboks Raphicerini 548
- Cape Grysbok *Raphicerus melanotis* 548
- Sharpe's Grysbok *Raphicerus sharpei* 548
- Steenbok *Raphicerus campestris* 549

- Beira *Dorcatragus megalotis* 551

Dikdiks Madoquini 552

Dikdiks *Madoqua* 552
- Salt's Dikdik *Madoqua saltiana* 554
- Silver Dikdik *Madoqua piacentinii* 554
- Kirk's Dikdik *Madoqua (kirkii) kirkii* 555

- Naivasha Dikdik *Madoqua (kirkii) cavendishi* 555
- Ugogo Dikdik *Madoqua (kirkii) thomasi* 555
- Damara Dikdik *Madoqua (kirkii) damarensis* 555
- Günther's Dikdik *Madoqua guentheri* 556

Gazelline antelopes Antilopini 557

Gazelles *Gazella*, *Eudorcas* and *Nanger* 558
- Dorcas Gazelle *Gazella dorcas* 559
- Speke's Gazelle *Gazella spekei* 560
- Cuvier's Gazelle *Gazella cuvieri* 561
- Rhim Gazelle *Gazella leptoceros* 561
- Red-fronted Gazelle *Eudorcas rufifrons* 562
- Thomson's Gazelle *Eudorcas thomsoni* 563
- Eritrean Gazelle *Eudorcas tilonura* 563
- Mongalla Gazelle *Eudorcas albonotata* 563
- Grant's Gazelle *Nanger (granti) granti* 564
- Tana Gazelle *Nanger (granti) petersi* 564
- Bright's Gazelle *Nanger (granti) notata* 564
- Soemmerring's Gazelle *Nanger soemmerringi* 565
- Dama Gazelle *Nanger dama* 566

- Dibatag *Ammodorcas clarkei* 568
- Gerenuk *Litocranius walleri* 569

- Springbok (Springbuck) *Antidorcas marsupialis* 571

Oribi Ourebini 573
- Oribi *Ourebia ourebi* 573

Reduncines, kobs Reduncini 574
- Rhebok *Pelea capreolus* 576

Reedbucks *Redunca* 578
- Mountain Reedbuck *Redunca fulvorufula* 578
- Bohor Reedbuck *Redunca redunca* 579
- Southern Reedbuck *Redunca arundinum* 580

Kobs *Kobus* 581
- Kob *Kobus kob* 581
- Puku *Kobus vardoni* 583
- Southern Lechwe *Kobus leche* 583
- Nile Lechwe *Kobus megaceros* 585
- Waterbuck *Kobus ellipsiprymnus* 586

Klipspringer Oreotragini 588
- Klipspringer *Oreotragus oreotragus* 588

Impala Aepycerotini 590
- Impala *Aepyceros melampus* 590

Alcelaphines, Topi and allies Alcelaphini 592
- Hirola *Beatragus hunteri* 593
- Bontebok/Blesbok *Damaliscus pygargus* 594
- Topi/Tiang/Tsessebe *Damaliscus lunatus* 596
- Hartebeest *Alcelaphus buselaphus* (incl. *lichtensteinii*) 598
- Brindled Gnu *Connochaetes taurinus* 601
- White-tailed Gnu *Connochaetes gnou* 603

Horse-like antelopes Hippotragini 605
- Roan Antelope *Hippotragus equinus* 605
- Sable Antelope *Hippotragus niger* 607
- Scimitar-horned Oryx *Oryx dammah* 609
- Beisa Oryx *Oryx beisa* 610
- Southern Oryx *Oryx gazella* 612
- Addax *Addax nasomaculatus* 614

Sheep and goats Caprini 615
- Barbary Sheep *Ammotragus lervia* 615
- Nubian Ibex *Capra nubiana* 617
- Walia Ibex *Capra walie* 618

INTRODUCTION TO THE FIRST EDITION

A field guide, like any other artefact, has an individual history and behind that a much longer generic history, in this case of books about African mammals. Such books are products of their times as well as of authors, and over some 500 years they reflect a changing history of ideas as well as a growing list of species.

Acknowledging debts to previous authors is important both for the data and for the ideas they have bequeathed. They also provide juxtapositions to help define what is new about one's own time and about one's own work. A major peculiarity of this volume is its genesis within tropical Africa. Any home-grown author has frequent reminders that books on African subjects originated abroad and that visitors are still major interpreters. Field guides do not escape that legacy.

For the people who first printed books, African mammals were mostly distant fable. Thus, mythological Bestiaries were the first of four main phases in the development of books about African animals.

The second phase is linked with Europe's expansion and colonialism. Animals, as in Europe, were little more than playthings of the privileged – game. Guides for this period began as hunters' 'Records of Big Game'.

In the third phase there was a change in vocabulary, 'game' became 'wildlife' as vast urbanised audiences received animal images and natural history stories in their homes and schools via books and television. The life histories of some popular species became familiar through the work of talented film-makers, naturalists and scientists. This phase coincided with the growth of mass tourism and the declaration of many magnificent national parks. Most current field guides are oriented to this period of expanding tourism and the growth of natural history as a major form of recreation.

Now we have begun a fourth era, marked by our self-discovery as mammals that have created their own extraordinary niche. It is a niche in which consciousness and technological power have brought responsibility for the fate of our own and all other life on earth. Space travel and satellite photography have given us a new awareness of our cosmic fragility and biological limitations, while problems created by pollution and environmental degradation have led to a new concern for the health of the biosphere. As we are ever more frequently reminded of the finite nature of natural ecosystems and their fragile complexity, Africa's uniquely rich 'biodiversity' has become a by-word. That biodiversity happens to include us, so that the ecology that nurtured our ancestors and helped shape our intellect and character demand that conserving Africa's diversity of plants and animals receives global respect and support. Such contemporary perspectives have shaped this field guide as they have my other books.

We live in a time of unprecedented accumulation of knowledge. Each year we learn more about living and extinct animals, about pre-history, human origins and processes that govern our past, present and future. From this cascade of new discovery has come the awareness that the survival of other animals is not entirely detached from our own. At the same time human penetration into previously untouched habitats has led to the spread of African primate diseases, such as HIV and Ebola virus, to cities and communities around the world, heightening our sense of proximity to, yet ignorance of, the natural world from which we have emerged so very recently. This is no aesthetic or historical conceit. Detaching ourselves from our biological past renders us less likely to understand our true nature. Dangerous repercussions follow in medicine and human ecology.

There is everything to be said for the observation of African mammals as recreation. As more people gain the ability and leisure to see African wildlife their pleasure and awe may be heightened by an awareness that what they are seeing would have been a familiar aspect of the existence of their ancestors, from ancient hominids to recent hunter-gatherers.

We call individual types of organism 'species' but, in the texts that follow, I try to give an indication of the countless structured relationships that each animal has with other species of animal and plant, and with the African landscape, its climates and a pre-history that stretches back many tens of millions of years. For a naturalist there are few greater delights than that of discovering for oneself the extraordinary fitness of animals for the niches they occupy. As observation reveals why animals are formed the way they are and how they relate to their surroundings one's sense of wondering enquiry can only increase. Curiosity may be the underlying motivation for the study of natural history but knowledge of African mammals easily leads on to more involved interests. As we come to understand how human beings have evolved within African natural communities we can gain a perspective on ourselves as an inextricable part of mammalian life on earth. This, surely, adds a new incentive to the joys of learning about African mammals.

In the nearly 20 years since the first edition of this guide was written, several revolutionary developments have taken place, suggesting that a new edition was due.

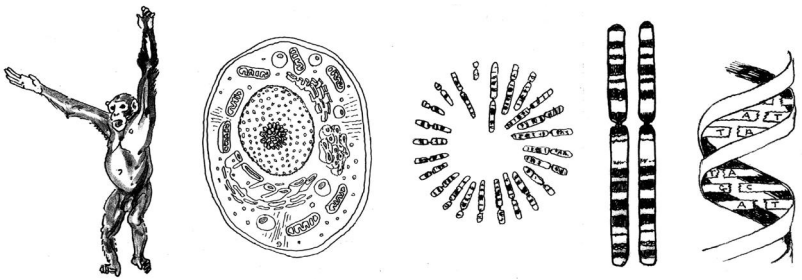
One important development has been a re-figuring of what our subjects mean in the context of human origins. It is now more fully realised that other mammals were dominant components of the community of plants and animals in which human ancestors, like any other mammal, struggled to survive over some millions of years. Our existence is proof of their success. We now know, with absolute certainty, that humans could *never* have evolved in the Americas or Australia. Only Africa (with some periods in and connection with Eurasia) could have generated a mammal with such a complex, convoluted evolutionary history. Only humans could have invented science and only a scientifically minded animal was equipped to enquire into its own origins!

Over the past 20 years scientists have posed just such questions and they have begun to develop tools for the task. Only in Africa have they a hope of finding answers and, step by step, discovering/recovering our *true* biological history. Many of the mammals portrayed here actually shaped aspects of human evolution (as competitors, predators, food, fur; as path-makers or sources of disease and epidemics). For 99% of history our ancestors had to fit in among them. Today mammals have to fit in among humans, but to fail to take our past into account for our future would be, and is, abject stupidity. This edition acknowledges the authority of that history; thus new information informs and extends this inventory of a continental fauna that is unlike any other. Among the more potent tools for this task is the science of molecular genetics.

During the past two decades the revolution in genetics has been gathering pace. Our knowledge of phylogenetic relationships has shifted from comparisons of external morphology and some inspired guesswork to much less subjective criteria. Thus a handful of very circumspect family trees in the first edition can be compared with this one, where more than a score of genetically based (sometimes dated), molecular phylogenies are on offer. These trees can be fallible and remain tentative, but our new-found ability to reconstruct genealogies continues to improve. It reflects a major advance in science (and, when applied to human origins, another step towards replacing poetic mythology with an inspiring, science-based re-telling of the story of how we came to be).

New genetic trees for all major mammal lineages have led to some significant re-ordering of the way organisms are classified and listed. It even led, in 1998, to recognition of an entirely new supercohort of mammals, the Afrotheria, with which this edition now begins. Indeed, the sequences and contexts in which mammal groups are now presented has been informed by the work of my many colleagues writing in *Mammals of Africa*, a handbook that I initiated in 1996 and led to completion in 2013. It is a measure of the pace of research and discovery that some of the most significant of all molecular phylogenies have only been published in the last year or so!

The genetic techniques and molecular clocks that have been developed over the past 20 years have greatly enhanced our understanding of biogeography and the evolution of species. This is because multiple genetic relationships, when plotted in space and time, help reveal pan-African dynamics of speciation. One pattern in particular recurs again and again, confirming that there are two major 'realms', effectively ecological and geographic 'islands', within this big, blobby continent.



Today, expressions of the 'science of shape' embrace internal organs, tissues, cells, enzymes and molecules. A living mammal contains multiple 'shapes', each of them expressions of self-regulating systems that range from gene to whole body. A chimp body contains about 100 trillion cells; each cell has a nucleus; each nucleus has 48 paired chromosomes; of every pair, one chromosome is from each parent; chromosomes consist of packed strands of DNA. Genes are DNA segments coded to make proteins.

Africa's 'up-ended L' shape has generated two axes, or biogeographic realms. One is an east–west axis that is dominated by latitudinal bands from forests to Sahelian steppes. The other is a north–south longitudinal axis running from Horn to Cape. (These realms are discussed further under the rubric of 'The Past' in the section on The African Environment.)

Yet another development has been discovery of many new species. A few are the outcome of modern penetration into remote regions or habitats (where local people were usually already familiar with animals only now proclaimed as new to science). However, other changes have resulted from new techniques, insights and theories leading to reassessment of earlier rankings. In many cases I pass on, and acknowledge these 'new' species (but, for caveats, see 'Naming Species'). Other scientific advances have enhanced our ability to comprehend the geology, topography and climatic past of Africa. Some of these are touched upon in my discussion of African environments.

Another very important development for Africa has been the grounding of national education programmes in science. This has made substantial advances in all progressive countries so that the educational role of this guide has also expanded. Affirmation of our commonality and of our recent biological origins in Africa is weakening some earlier, once-dominant, non-scientific cultures. Most notable among these were actual or would-be empires or theocracies, all of non-African origin, that trivialised, mythologised, commodified or infantilised animals. With the certainty that we, *Homo sapiens*, came out of Africa and evolved within its ecological communities, our cousin primates and other mammals have had to be taken more seriously, as has their conservation and the plight of Africa's natural environments. A reference book, such as this guide, serves to increase people's access to such essential and updated information. Even more important, it serves to reveal just how extraordinary Africa is – how unlike any other continent. In spite of this awareness, a new dilemma for Africa is the birth of a cosmopolitan generation that fails to appreciate this fact. It is a generation many of whom, unwittingly, collude in degrading Africa to the semblance of any other sorry continent.

A guide such as this one also has a role to play in Africa's current openness to the world. So I hope it will help ease access to some of the wonders of this unique continent. The past 20 years have seen a great expansion in tourism and the development of first-class national parks, reserves, lodges, conservancies and educational programmes. Botswana, once an environmental pariah, now has fine parks, conservation education in schools and a flourishing and much envied tourist industry that provides numerous forms of employment and a more environmentally oriented culture. Botswana's leading role in conservation is structurally linked to its rating (by Transparency International) among the top countries in the world for probity and sound governance.

By contrast, several African countries rank among the most corrupt in the world, namely Somalia, Sudan, Libya, Equatorial Guinea, Eritrea and Chad (Transparency International). As a result, all these countries have vestigial educational opportunities, are losing or have lost much of their large mammalian fauna and earn near-zero income from visitors. During the last two decades Ethiopia's globally important natural estate has suffered horribly under very poor leadership. Cameroon, biologically one of the richest regions on this planet, has become one of the most tragic of all African countries. Where I once walked in forests of unrivalled diversity and endemism, sterile rubber trees, oil palms or pineapples now grow in rows that stretch to the horizon. The last pathetic remnants of its forest fauna, like that of many other equatorial countries, hang, for all to see, on scaffolds beside main roads, their contorted, maimed and mistreated bodies a dying reproach to the cruelty and rapacity of humans.

National education and research programmes as well as the larger conservation community can all be faulted for neglecting to educate local people, such as those of south-western Cameroon, about the global significance of their own backyard. Some vision, better education and more local involvement in conservation could have opened new opportunities in research, teaching and in tourism infrastructure. Before it is too late, Cameroon and many other nations need to develop an awareness that Africa has more to offer the world than any outsider can offer Africa.

In conclusion, the first edition of this guide was written in a more leisurely era. Today, science has become the fastest-moving frontier in contemporary culture. Its commercial spin-offs are legion but, among them, we can already identify aspects of modern agribusiness that threaten the survival of many mammals and their habitats. The welfare of many rural people in Africa is no less at risk. In an ever-accelerating, ever more global and ever more predatory world we *must* identify and hold the main agents of destruction accountable. We must also invest in ecological research and environmental education – a more knowledgeable respect for nature in the mother-continent.

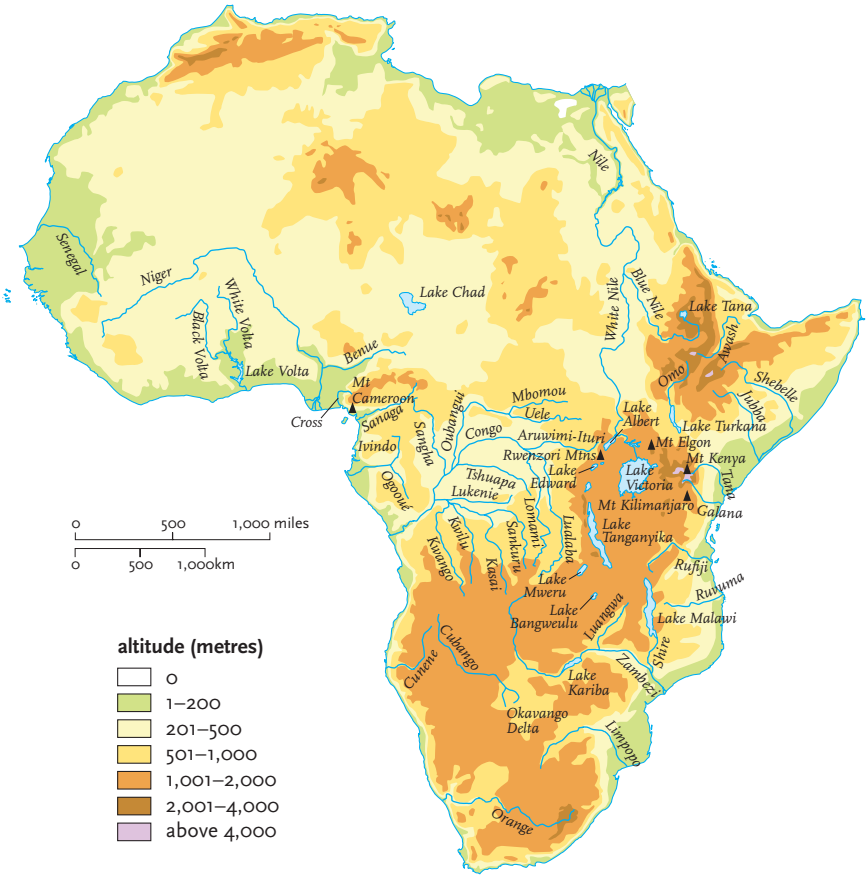
NAMING AND MAPPING SPECIES

This field guide lists more than 1,160 mammalian species from Africa and maps the majority. While it is certain that more species await discovery (especially among bats, shrews and rodents), the overall scale and composition of Africa's mammal fauna is now reasonably well known, even if names sometimes chop and change. As the checklist and guide to a continent's known mammalian fauna, the pages that follow have been brought up to date and some of the latest ideas about classifying and naming species have been incorporated. There are descriptions, illustrations and maps of all known species of primates, small groups, such as pangolins and hares, all large mammals, carnivores and squirrels. All genera of shrews, bats and rodents are described and illustrated but limitations of space have precluded species profiles in some genera with many species (for example, there are more than 100 species of *Crocidura,* the white-toothed shrews, and among some 100 species of gerbil are at least 36 species of *Gerbillus*). The written profiles of mammals are supported by a full-colour illustration (generally of an adult male), skull drawings of smaller mammals, and a map showing the animal's overall range. Bloomsbury Publishing has kindly authorised reproduction of the distribution maps used in this guide's sister publication, *Mammals of Africa*, with, where necessary, some additional, revised, enhanced or 'zoomed-in' maps. In some exceptional cases, past and present distributions are presented.

Political map of Africa.

Naming presents innumerable challenges for a work such as this. The classification and nomenclature first published by Linnaeus in 1758 provided a hierarchical system and a set of Latinised scientific names that could be applied to all organisms and be used by all nationalities. This has ensured that, no matter what language is used, all naturalists and scientists can be certain of referring to the same animal or plant so long as it has been correctly identified. Vernacular names are therefore much less important than scientific ones. The former often vary or have alternatives while the latter are arrived at by strict rules of priority and can only be changed when the rules are shown to have been broken by the application of a mistaken name. Many mammals have been given informal regional names and some of these are retained in this edition, but names used in the first edition have been augmented by ones published in *Mammals of Africa*. In addition to English and French, German and Swahili names have been given where possible.

Today new genetic techniques are refining the naming process, sometimes showing that long-recognised separate species should be amalgamated or, more frequently, subdivided. Molecular phylogeny also allows recognition of subgroups and species clusters. Where 'molecular clocks' can be attached to these trees the timing of branch internodes can be assessed. These, in turn, often suggest a re-ordering of the sequences in which species or groups are presented to the reader: more conservative taxa first, most recently evolved last. Changes in names and sequences can be confusing but, in the long run, naming and ancestral trees will, eventually, become more,



Altitudes and major rivers of Africa.

not less, stable. All changes in nomenclature still have to conform with well-tested Linnaean rules.

In the past two decades a dozen new species of primates have been discovered (or named/renamed on the basis of new information): a likely ur-mangabey on a Tanzanian mountain, some guenons in central Africa and still more galagos (their identities first signalled by sound recordings of their distinctive voices). Furthermore, genetics has led to re-groupings or revisions of species by specialists. New genetic evidence has created or abolished higher taxa, ranging from the genus to the family. These higher classifications help us to allocate individual species to their natural groupings. I have therefore included brief profiles of most tribes and families. To avoid unnecessary repetition, subgroups, infra-groups and super-groups are sometimes ignored or subsumed within larger categories.

Linnaean systematics were originally designed, like conscientious book-keeping, to bring order to the apparent chaos of diverse species. An almost incidental by-product of this hierarchical system has been the provision of a useful indication of relationships and hence a guide to how species have diversified and lineages branched out. As taxa move higher, a single species is joined by more cousins, each step embracing more and more ancestral categories. By way of illustration, the following represents the position of human beings within the Linnaean structure:

Class Mammalia
Subclass Eutheria
Order Primates
Suborder Haplorhini
Infraorder Catarrhini
Superfamily Hominoidea
Family Hominidae
Subfamily Homininae
Tribe Hominini
Genus *Homo*
Species *Homo sapiens*
Vernacular name Human Being

Reflecting on the family to which we all belong, Darwin, in 1837, wrote "animals, our fellow brethren in pain, diseases, death, suffering and famine – our slaves in the most laborious works, our companions in our amusements – they may partake of our origin in one common ancestor – we may be all netted together." Thus do deep truths lie bedded within the simplest outline of taxonomy.

Sometimes relationships between species are so close that the cluster is called a 'superspecies' or 'species-group'. Likewise, a genus is sometimes subdivided into subgenera. Similar clusters can be found at higher levels. For example, rodent diversity is so complex and layered that it requires numerous subfamilies. Likewise, a most useful taxon for antelopes is the tribe (a lower-level clustering that implies a more recent evolutionary radiation than that of the rodents).

Judging which taxonomic suggestions to embrace and which to reject has brought new perspectives to the old question 'What is a species?'. Mammals and primates are *our own*, parental branches on the vast tree of life and we, as global modern humans, represent that ultimate unit we call a species. Our unit emerged, as one among many, on a twiglet. This, in turn, belonged to a twig and so on, cluster by cluster, merger by merger, back to the mother tree – so asking 'What is a species?' is no trivial question. Trees and the dates for divergences are still tentative and subject to human error, but the reality of ancestry is incontestable.

Controversies over naming are still acute, especially when it comes to 'splitting' or 'lumping' species. This is most notable for ungulates, where a particularly severe application of the 'Phylogenetic Species Concept' (PSC) by Groves and Grubb (2013) has nearly doubled the suggested tally of species. One of the virtues of PSC has been to put a high value on distinctness at the population level. Over-zealous application of this concept, however, results in a huge proliferation of 'new' species because PSC explicitly ferrets out the *smallest* populations that show consistently identifiable differences. Thus small founder-effects can elevate tiny, labile populations to rank as species regardless of the ecology, behaviour or boom-and-bust dynamics that influenced

their distinctness. More critically, 'PSC species' are mainly erected on the examination of museum specimens and distinctions between major and minor adaptive traits tend to get lost along the way. Thus naming gets immured in laboratories and museums and the most generally appreciated unit of taxonomy and nomenclature, a species, can get multiplied exponentially. Remembering to which, among a dozen PSC species, some local population might belong can acquire a spurious primacy. The confidence of non-scientists in their ability to identify an animal can be undermined by a plethora of species names. This contradicts a central purpose of this guide, which is to bring more clarity, not less, to the process of identifying mammals. A primary aim of this guide is to widen access to and share delight in the process that has given life to us and to all our fellow mammals. A guide such as this one invites confident participation, most particularly among my fellow Africans, in that finest of all recreations – natural history. In the pages that follow I have generally used the arrangement we followed in *Mammals of Africa* or, where appropriate, retained the format followed in the first edition of this guide. I comment on those subspecies that have recently come to be regarded as species by PSC taxonomists and I repudiate those most extreme among them that altogether reject subspecies as a category!

Much more interesting than squabbles over ranking are new links between name, lineage, distribution and evolutionary age. The best and most recent example of this concerns the Afrotheria. The very name (coined by Alan Walker) identifies a supercohort of mammals with its continent of origin. The genetic research that identified this lineage, when correlated with known-age fossils, has revealed that its origins go back well over 80 million years. Its six component orders began to differentiate early on, and one group, the sengis (Macroscelididae), is particularly ancient. Thus the supremely elegant giant sengi, has, with some justification, been called a 'living fossil' (I prefer the title 'ecological elder'). Its genus, *Rhynchocyon*, is already recognisable in 20-million-year-old fossils. Sengis are so distinctive that they differ more from any other living animal than, say, a pig does from a giraffe.

By contrast, the long-faced, short-necked Kongoni antelope, with its bizarre horns, is known to have appeared only within the last one million years. Fossils not only tell us that the Kongoni is a relative newcomer but they reveal that these large, oddly proportioned antelopes derive from much smaller, gazelle-like ancestors and were in an actively speciating phase when cattle and their owners arrived to displace them.

The recent evolution and graceful ancestry of Kongonis could never be inferred from the living animals alone, nor could superficial scanning reveal the unique conservatism and long ancestry of the giant sengis. These examples show that the process of identifying and naming a mammal not only invokes other sources of information, it is essentially the same process that names and classifies fossils and allows us to make sense of the great mammalian radiations in deep time. Yet a catalogue of ancient bones remains just that until each extinct animal's place has been found on the tree of mammalian evolution. Today, Kongonis are more numerous and have more impact on the landscape than giant sengis, yet, when it comes to evolutionary trees, their status is very different. Kongonis are represented by tiny, outermost twiglets while sengis derive from a long, thin branch that comes straight from the trunk. The tree on p.47 summarises current thinking about relationships between the major groups of mammals.

Mammal groups divide into those that were present in Africa before the first of a series of more recent immigrations from other continents (between about 23 million years ago (mya) and the present). Among the former are afrotheres and the ancestors of apes and monkeys. Among the colonists from Eurasia are hares, a succession of rodents, most carnivores and the odd- and even-toed ungulates. Among the immigrants, canids and Cheetahs originated in the Americas, as did zebras, which are among the most recent of all arrivals (via Asia, of course).

It is surprising to learn that the stock for many groups that now typify African fauna came from Eurasia or beyond, but other continents, too, owe their elephants, their primates and many other immigrants to Africa. Understanding all these ancient comings and goings depends on the interpretation, classification, naming and dating of both fossils and genes.

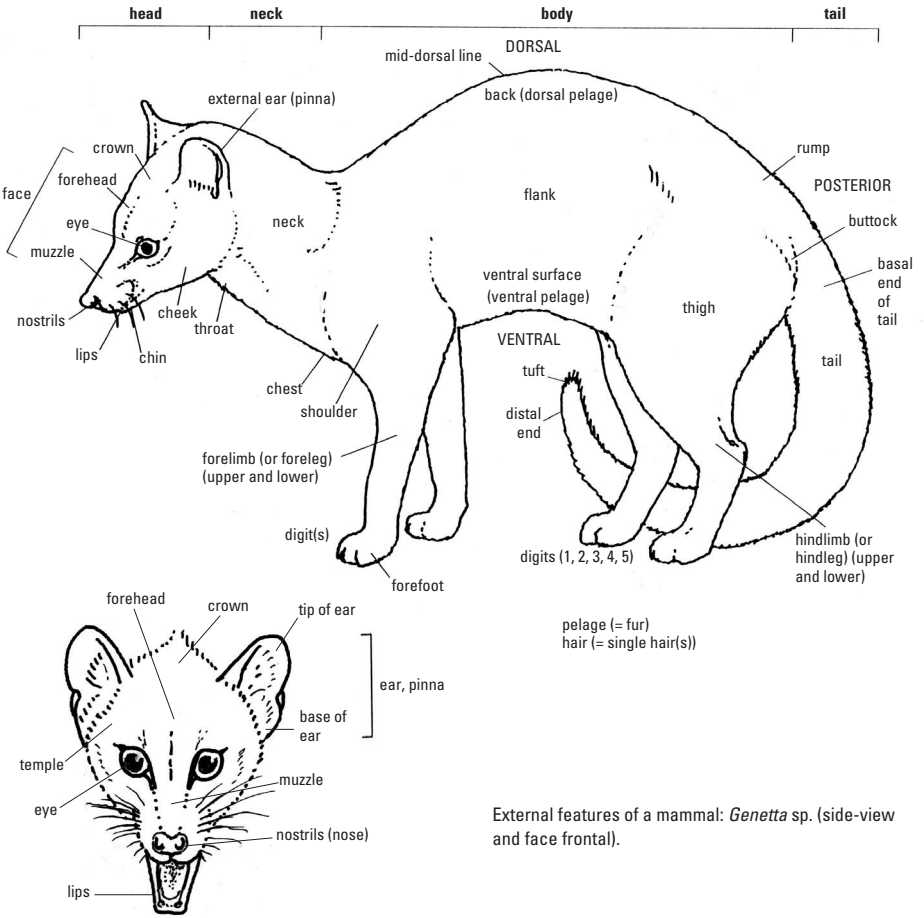
It is as well to remember that a great many living species, including so-called 'living fossils' that have survived the eons, are now, suddenly, heading for extinction at our hands. The pace of exterminations by humans now threatens to take on apocalyptic proportions unless we develop the will to create a more intelligent and humane culture that can take action on a global scale.

USING THIS GUIDE

Correct identification of an animal depends upon the nature of the encounter. In the field the great majority of clues are indirect but, in the guide to a fauna of well over 1,100 species, an inventory of tracks, outlines of burrows, forms of excreta etc., would be impractical. This guide is therefore limited to concise verbal descriptions and detailed full-colour illustrations (sometimes backed up by keys or diagnostic details in the skull, teeth or pattern).

Mammal books that emulate bird books with an item-by-item enumeration of colour patches, long or short crests etc, are not well suited to the more subtle variation and complexity of most mammals. Comparisons with familiar animals, such as dogs, cats, sheep etc., are rendered useless by the sheer diversity of African mammals. Therefore, the colour plates in this guide aim to assist identification by illustrating something of a species' 'jizz'. Jizz is the naturalist's word for the total sum of form, colour, stance, silhouette and movement that allows an accurate assessment of a species-specific shape. Ritualised displays often serve to emphasise a species' peculiarities. Some plates illustrate such postures.

While I hope the 'once-in-a-lifetime' visitor to Africa will find this guide useful, it is designed to help those with more sustained and involved interests in African mammals. It aims to outline the ecology and evolutionary history of mammals and is intended as a celebration of the great diversity of their forms. The guide includes summary descriptions of behaviour but readers seeking more



External features of a mammal: *Genetta* sp. (side-view and face frontal).

detail should refer to Richard Este's excellent *Behaviour Guide to African Mammals* and to this guide's sister publication, *Mammals of Africa*.

Species profiles present information under a set of standard headings. After scientific, English and other names are: Measurements, Recognition, Geographic variation, Distribution, Habitat, Food, Behaviour, Adaptations and, finally, Status. An abbreviated format is used for species or genera that are poorly known or have closely related species already described in greater detail. For profiles dealing with tribes, families or higher categories I have adopted a more flexible approach. A similar range and sequence of information is summarised, but formal headings are included only in longer profiles. These are: Recognition, Genealogy, Geography, Ecology, Natural History and Adaptations.

For the species profiles, the subheadings in sequence are:

MEASUREMENTS Head and body, HB; tail, T; total length, TL; standing height, SH (where appropriate); shoulder height, Sh. ht (where appropriate); ear length, E; forearm, FA (for bats); weight, W.

RECOGNITION This heading deals with what makes a species (or group of related animals) easy to recognise, with a focus on those characteristics that are unique to that species or group.

GEOGRAPHIC VARIATION (formerly Subspecies) When a species shows well-defined geographic differences these commonly receive recognition as subspecies. As more and better genetic evidence becomes available some former subspecies may be reclassified as full species. Some such revisions have found support in this edition. Others await further genetic evidence, yet others (notably *Damaliscus* populations) are unlikely to find general acceptance and are rejected. When a species varies clinally across its range this is noted wherever it is likely to affect recognition.

DISTRIBUTION Description of distribution is accompanied by a map, and special geographic features may be noted.

HABITAT Physical and climatic determinants of habitats are mentioned, with the central focus on vegetation and, for the smaller species, their micro-environment. All habitats can change, advance or contract under changing climates and, of course, under the impact of fire, grazing or agriculture. Such changes have not been taken into account in mapping the distribution of species, nor for the major vegetation zones, as shown on p.37.

FOOD Wherever known, dietary preferences are summarised by general characteristics (rather than long lists of species).

BEHAVIOUR Most profiles describe a 'nugget' of behaviour that is typical or diagnostic of the species. Where relevant, reference may be made to social structures, modes of communication, activity cycles, senses, gaits and breeding.

ADAPTATIONS Special adaptive characteristics that help to define the species, its niche or species-specific features of its anatomy or physiology.

STATUS Here an assessment of a species' conservation status may be given as published by the IUCN Species Survival Commission. The main categories used are 'extinct', 'extinct in the wild', 'critically endangered', 'endangered', 'vulnerable', 'near-threatened', 'least concern', 'data deficient' and 'not evaluated'. For some species the CITES listing is also given. As few African countries have been accurately evaluated for any but the commonest 'game' animals, most assessments need to be viewed with caution. The real situation may be much better or worse than recorded and the status of those species that are most vulnerable to the destruction of their habitat or to unregulated hunting is changing quite rapidly. Where IUCN assessments on status have yet to be made, a consensus of contemporary views from relevant authorities is offered.

FINDING AND RECORDING MAMMALS

The larger mammals, particularly non-forest species in well-protected national parks, are generally easy to view (sometimes on foot, but more usually from a vehicle or hide). Outside protected areas they can usually be seen only at some distance. The great majority of African mammals are small, very shy, mainly nocturnal species. Naturalists and scientists can now employ sophisticated methods to

study such species, notably camera-traps, night-vision glasses, electronic sensors, radio- and spool-tracking, bat-detectors, hidden recorders and satellite tracking devices. However, for both the amateur naturalist and scientist alike, a good pair of eyes, a pencil and a notebook can be all that are required. To augment the naked senses and provide permanent records of momentary events, binoculars, a sound-recorder and hand-held digital camera are useful adjuncts. Camera-trapping has become a particularly exciting and informative technique for both amateur naturalists and professional biologists.

Anyone interested in mammals should keep notes and records. Every human–animal encounter has some significance, even apparent 'accidents', such as an otter-shrew in a fishing net, an African Wild Dog killed by a speeding lorry, or a tomb bat drowned in a school cistern. Indeed there are aspects of the biology of such animals that might never have been discovered but for such mishaps.

Most mammals are encountered indirectly, most commonly by their tracks, diggings, excreta and feeding sites. Bones and skulls are occasional finds but, sadly, some of the richest sites for animal remains, often of rare and little-known species, are on urban market stalls or beside main roads. This plunder is a growing menace in all those African countries that effectively permit the commercial exploitation of 'bushmeat' for urban markets. In the first edition I noted that a campaign against this highly damaging, and mostly illicit, trade was gathering momentum and deserved the widest possible support. Sadly, and disgracefully, this momentum has stalled in several major nations that are responsible for conserving or regulating precious biodiversity in Africa. It is to be hoped that Ethiopia, Cameroon, Bioko, France and China, among many others, will soon reform and stop turning a blind eye to the pillage of Africa's most precious resources.

We owe to amateur naturalists most of what we know about mammals in Africa, much of it recorded indirectly from keen African observers and hunters. From the earliest foreign explorers to contemporary civil servants, naturalists have recorded countless interesting details. The collators of this accumulated knowledge have, for the most part, been non-Africans writing for non-African audiences. Today this is changing. Fireside gossip is no longer the preferred medium for communicating indigenous knowledge about local animals. African naturalists and scientists now publish for international as well as for local audiences. This is the context for a new generation of field guides, including this one.

The authority for this book lies in an African childhood and a lifetime of research, travel, university teaching and writing on various aspects of evolution in Africa. My qualifications for the task lie with several previous works, most notably with *East African Mammals: An Atlas of Evolution in Africa*, *Island Africa*, *Self-made Man*, *Lowly Origin* and, most recently, as lead editor for *Mammals of Africa*. Most publishing projects rely on author, studio artist and graphic workshop to supply the texts, illustrations and maps for their cooperative enterprise. The dislocations are obvious to any careful analyst of the end result. This is particularly true for my own generation of scientists, whose literary and literal education was often at the cost of our visual intelligence. The earlier edition of this guide, *Island Africa* and *Mammals of Africa* have all broken new ground in that an author is also illustrator, cartographer and even designer. I trust that the results speak for themselves.

I hope this field guide will accompany solitary naturalists on their excursions through Africa's landscapes. I also hope it will reach new potential audiences in schools and cities. Most critically, I hope that new knowledge, such as is incorporated here, might reach and influence future policy-makers, even politicians. Contempt for their own natural environment and for nature (often combined with awe-struck obsession with novelties from abroad) characterise far too many of today's policy-makers. Yet there are encouraging trends, particularly in southern and eastern Africa, where there are new demands for a working knowledge of ecology. Rapid growth of economically vital tourist industries (mostly founded on wildlife and natural habitats) ensures that the new enthusiasts and wildlife experts are teachers in schools and universities, wardens, rangers, couriers and drivers, in school buses and minicabs or on park outings, sometimes students educating their parents! I hope that my work will help these new persuaders to convince both local people and visitors alike of the significance of African habitats and fauna. Here were the environmental settings within which our ancestors flourished; here our origins were tied into the mammal communities of which we were once a part; here were the settings within which our ancestors developed knowledge and experienced beauty and awe. In our uniquely rich natural heritage we can retrieve something like ancestral wisdom but also discover and develop new and unexpected sources of delight, wonder and understanding.

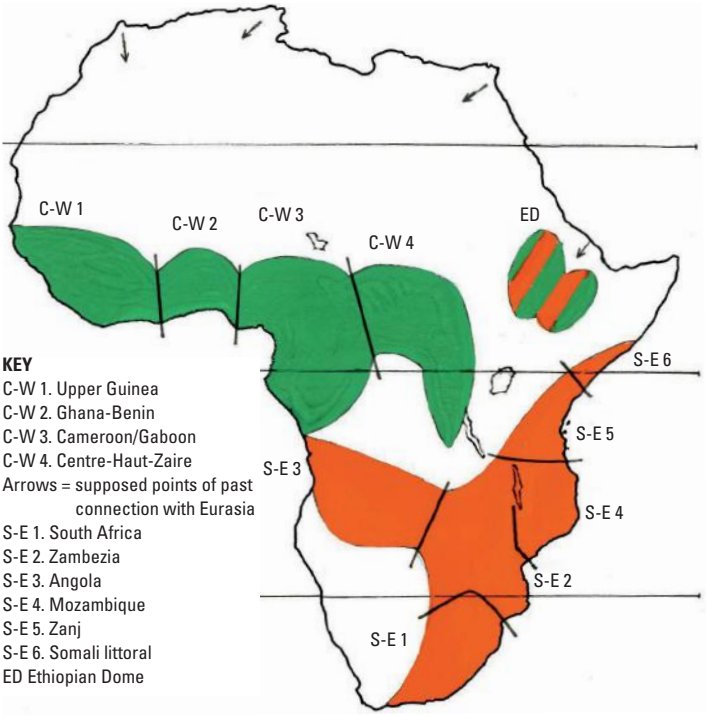
THE PAST

All life is built upon what went before and the lives of organisms differ greatly in duration. Trees being felled today were growing before the Pyramids of Egypt were built. A mouse born this year will be senile next. You and I come somewhere in between these extremes. Yet it is important to remember that the broadest outlines of modern habitats, deserts, forests and various intermediates, were already well developed some millions of years ago. However, the relative importance of, say, forest or desert has fluctuated widely, following huge swings in global climate that go back more than 15 million years but are best known for the last 1 million years.

Today's extensive rainforests and warm savannas are exceptional and we live in a period close to the wetter and warmer end of the scale. The last major spell of cold, dry weather peaked in Africa about 19,000 years ago, coinciding with the last global ice age. This was the most recent of more than 20 ice ages, each of which brought dry weather to most of Africa.

At such times lowland rainforests and all their associated biota would have retreated to especially favoured spots in Liberia, Cameroon, eastern Democratic Republic of Congo and Tanzania, all close to the Equator. (Of these countries, only Tanzania has made adequate efforts to live up to its responsibilities as custodian of global treasures.) The communities of animals and plants that are now restricted to cool, relatively dry belts on African mountains would then have spread over very extensive areas. Mammals that are now restricted to temperate or cool areas (like the Springbuck in southern Africa or the Gelada in Ethiopia) are known from fossils to have once been abundant in today's tropical areas.

The gross pattern of climatic change is a simple one. Dry habitats have tended to expand or contract from north to south and vice versa, sometimes creating dry corridors that crossed the



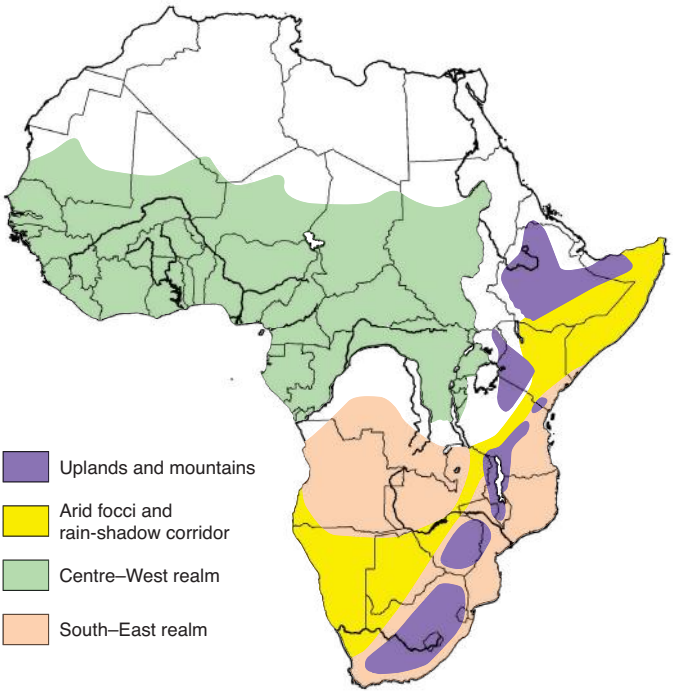
Division of sub-Saharan Africa into two major evolutionary realms. 1. Humid, latitudinal 'Centre–West' (C–W). 2. Drier longitudinal 'South–East' (S–E). It is postulated that populations originally confined within either realm may extend into intervening areas (most notably to the Ethiopian Dome) or may eventually spread more widely as new species. Past changes in climate, augmented by geographic barriers, have subjected each realm to further (and changing) subdivisions or conjunctions.

entire continent. Warm, wet periods on the other hand cause forests to pulse on an equatorial east–west axis. The result has been repeated fragmentation of both wet and dry habitats and, with that fragmentation, populations of animals and plants have suffered repeated bouts of isolation. While relatively stable species have simply pulsed with their habitats, many others have made local adaptations and speciated or subspeciated.

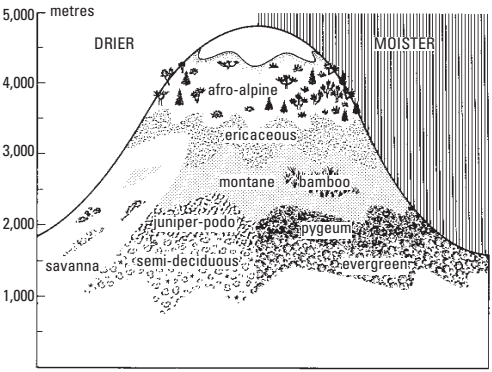
Many animals and plants have diverged into two distinct/discrete populations, one in each of these biogeographic realms (see map opposite and refer to maps for baboons, Giraffes, porcupines and wild pigs for examples). Furthermore, each of these realms fragments still further and the distribution of subspecies or distinct populations often corresponds with some, or all, of these subdivisions (see key to subdivisions opposite).

The natural barriers separating such sibling populations vary but the clearest and most frequent boundaries are the lower Congo R., Lake Tanganyika and a long arid corridor that links the dry Horn of Africa with Namib/Kalahari drylands in the south-west. This corridor is essentially a rain-shadow behind a long (and once very high) chain of uplands stretching from the Taita hills in Kenya through the 'Eastern Arc' and Malawi Rift mountains to the Kalahari and Namib drylands. These uplands intercept moisture blown in off the Indian Ocean, causing the land lying in their western lee, their 'shadow', to suffer desiccation. The barrier effect of this rain-shadow has been most decisive for moisture-dependent biota at tropical latitudes and during glacial periods. In spite of its porosity for some species, the arid corridor that skirts Mt Kilimanjaro and runs on to the south end of Lake Tanganyika is now recognised as a convenient marker for a boundary of great biogeographic significance.

Subdivision of sub-Saharan Africa into two realms or 'islands' helps to explain the extraordinary diversity of species and subspecies, especially among equatorial mammals. Correlating the distribution patterns of many primates, squirrels and small carnivores with their phylogenetic trees suggests how climatic changes drove speciation. Many now isolated populations belong to earlier branches of their lineage: they now live in corners of their previous range. These localities are often identifiable as refuges, sometimes high on cool uplands, sometimes in enclaves within much more extensive, but newly grown forests.



Arid corridor between NE and SW Africa. A long succession of highlands intercepting humidity off the Indian Ocean have generated this corridor of rain-shadows.

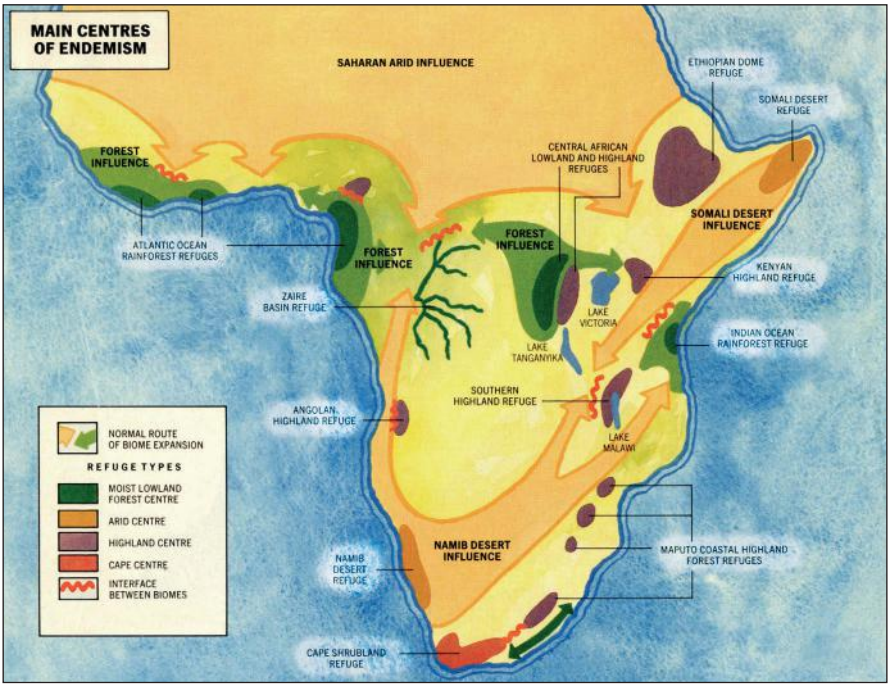


Montane and forest vegetation in relation to altitude and moisture.

Amid all the changes there have been identifiable areas of stable climates. Somalia has always been a hot, dry spot, Namibia a cool one, Cameroon consistently warm and wet, Ethiopia high and dry, and Rwenzori high and wet. The coast and mountains of equatorial East Africa have always caught rain from the Indian Ocean while Liberia and Cameroon have caught it from the Atlantic. At the centre, the Rwenzori Mountains are moistened all year from both east and west.

Where major variables meet along consistent boundaries many biological niches become possible. Wet meets dry, high meets low, cold meets warm. Faces of hills, mountains or escarpments tilt towards rain or rain-shadow, towards moist or desiccating winds. Many localised species survive in these narrow zones, which are found on mountain slopes in southern and south-west, north-east, eastern and central Africa.

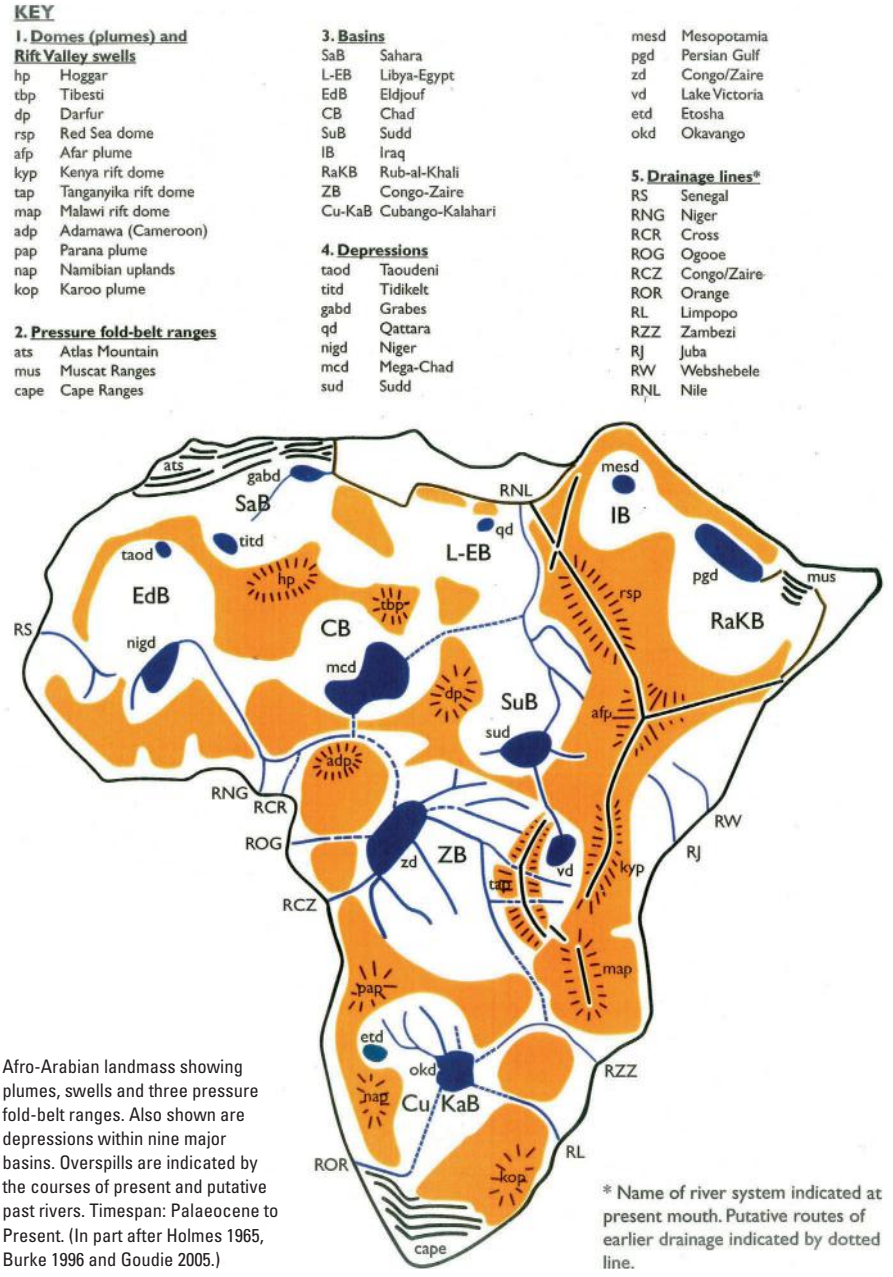
These narrow corridors and the stable foci, both wet and dry, are 'centres of endemism' and they give a special interest to areas such as the Cape, the equatorial coasts and mountains, Ethiopia and Somalia as natural 'reserves' or refuges for rare and conservative species. The details of their morphology or physiology, even their localised presence and survival, are only comprehensible in terms of their past, their 'natural history'.



Main centres of endemism in sub-Saharan Africa. Showing N–S, S–N expansion and contraction of arid foci and E–W, W–E expansion and contraction of humid foci. Intermediate ecotypes (often narrow) are typically located along interfaces between these biomes and on piedmonts of upland massifs. A more extensive exploration of the dynamics of fauna and flora is available in *Island Africa* (Kingdon 1990).

PHYSICAL LANDSCAPE

All continents are plates of once molten material that have become crusts, which swing and slither over the Earth's surface. Africa is the largest and, in terms of its global position, the least mobile fragment left over from the break-up, between 180 and 110 mya, of the super-continent Gondwanaland. Its other fragments, South-East Asia, Antarctica, Australia, India, South America



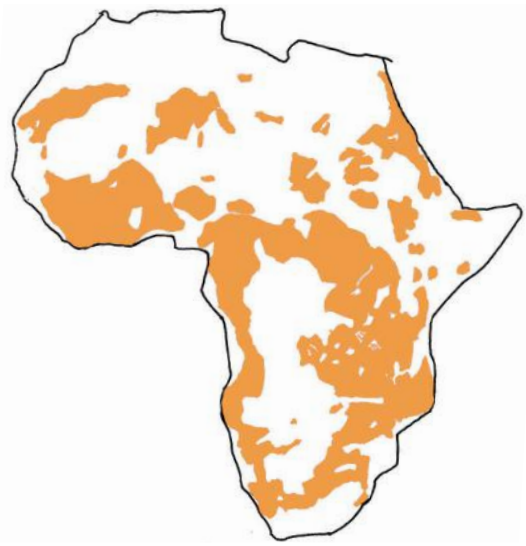
Afro-Arabian landmass showing plumes, swells and three pressure fold-belt ranges. Also shown are depressions within nine major basins. Overspills are indicated by the courses of present and putative past rivers. Timespan: Palaeocene to Present. (In part after Holmes 1965, Burke 1996 and Goudie 2005.)

* Name of river system indicated at present mouth. Putative routes of earlier drainage indicated by dotted line.

and Arabia, peeled away, piece-by-piece, and now are mostly scattered across the southern hemisphere. India broke away about 120 mya, South America had separated by 110 mya, while Arabia began to break away about 35 mya. The residue of those serial fractures still exists in the form of raised land along Africa's eastern and western margins. Those marginal mountains, especially the Red Sea hills (paired with the escarpments of western Arabia), not only hint at the mechanism underlying Gondwana's fragmentation, they illustrate the dynamics that have created a geology and geomorphology that is unlike that of any other continent. The overall continental pattern is one of swells around a scatter of basins. The swells are thought to be the product of relatively stable plumes, or 'hot spots', down in the mantle, which have thrust up the land surface above them.

Because they drift in a particular direction (northwards for Africa), tectonic plates acquire linear scars wherever a mantle plume beneath punches upwards. Thrust up into a ridge, some such elongated domes split open to form the celebrated Rift Valleys of Africa. Rift valleys are the beginnings of seas and, eventually, oceans.

Domes and swells vary greatly in height and extent, and only sometimes fracture to release volcanism. One plume, beneath the Rwenzori Mountains, has pushed ancient bedrock up to over 5,000m and pock-marked the neighbourhood with volcanoes and craters of all sizes, but most swells, such as those that surround the Okavango, Congo, Sudd, Chad and Eldjouf basins, have raised rafts of crystalline basement rocks over very extensive areas with little or no volcanics. Erosion has exposed bedrock over much of these shallow swells, so they have very low fertility and, in the near-absence of nitrogen in the soil, selection has favoured the evolution and dominance of leguminous plants that can fix atmospheric nitrogen. These nutrient-deficient landscapes, typified by the Miombo woodlands (made up of leguminous trees), support fewer mammal species, which generally live at relatively low densities. As a result, large predators are scarce and the main large antelope in Miombo, the Sable Antelope, *Hippotragus niger*, survives on a grazing strategy that probably resembles that of the low-density desert antelopes from which it likely descended. During the rains Sable crop thin, short grasses and herbs growing under the woodland canopy. Then, as the wooded slopes dry out, they seek out termitary/hardpan fringes where precious nutrients leach out (or are dredged up by termite action) and there is sufficient moisture to stimulate green growth (an equivalent ecotone in western Australia is known as 'pindan'). Before the rains return, the herds (averaging 15–20 animals) are sustained by green flushes that follow burns in the cotton soil '*mbugas*' (wide, flat, grassy valley bottoms). The search for graze takes Sable over ranges of up to 118km^2 but this antelope's survival is predicated on the rarity of Lions, hyaenas and hunters in Miombo. While Lions and scarce green grazing are immediate factors in Sable biology, it has been the underlying geology of Africa's ancient Precambrian 'shield' that ultimately governed the evolution of this splendid antelope.



Map of Precambrian surfaces in Africa.

The great Rift Valley system has derived from several phases of uplift down the eastern side of Africa. The most recent major upheavals have been dated to 22 million, 6 million and 2.5 million years ago. The largest dome, 400km wide, embraces Ethiopia and Yemen. South of the Ethiopian dome, stretching thousands of kilometres and in a jagged course from north to south, uplifted land has split along axes to form rift valleys that average about 40km in width. Associated volcanics have spewed out lava over extensive areas and thrown up volcanoes such as Kilimanjaro, which is 5,895m high. Earlier volcanoes have eroded away and deposited deep sediments. Cycles

of erosion and deposition have created dramatic landscapes of mountains, deep valleys and gorges. Recent volcanics and the tipping of extensive land surfaces have changed the direction of rivers and diverted waters from one basin to another; the River Nile, finding every exit to the Indian Ocean blocked by uplift, has had no alternative but to flow north, in the process becoming the longest river on earth. Among many dramatic and consequential developments of uplift are rift valley lakes and periodic ponding in other basins. Some of these have been ephemeral. L. Chad in the Sahara has expanded and contracted more than once, the Qattara, Tidikelt and Makgadikgadi depressions, once lakes, are now salt pans.

Distribution of rivers and lakes in Africa.

L. Victoria began as a result of the blockage of two large tributaries of the Congo R. Due to uplift in what is now Rwanda and Burundi the waters of these rivers ponded back, creating the present very shallow lake. All these lakes have been important as barriers to the spread or mixture of mammal populations. In the Congo basin a very large lake persisted for several million years until the mid Pliocene. Then, cut-back by a small Atlantic river created a new drainage line, emptying the Congo basin of its huge lake. This relatively recent event has left a pattern of distribution that makes the Congo R. one of the most consistent and major biogeographic boundaries in Africa (in spite of the vegetation north and south of the river being superficially indistinguishable). Overspills from the long-lived and always very wet Congo basin may have cut exits in several directions (even, perhaps, to the south-east, into today's lower Zambezi). Other possible exits were northwards into today's Benue valley and, later, down the Ogooué valley, which is disproportionately deep and wide for its contemporary catchment area.

Another major biogeographic boundary, along the Cross R. in east Nigeria, may also find its explanation in the re-routing of a once major river emptying down the valley of the Cross R.

Other geological events have shaped recent distributions. In the Virunga Mts area, major eruptions about 22,000 years ago blocked and deepened L. Kivu. Subsequent eruptions, one as recent as 9,000 years ago, are thought to have depleted fish and reptile fauna and it is possible that release of vast accumulations of methane gas in L. Kivu combined with tremors and eruptions to send a poisoned fireball down over the slopes west of L. Kivu. In any event, this area has many unusual anomalies of mammalian distribution which require research and explanation.

In contrast to these dynamic and recent events are the eroded, geologically ancient landscapes of the Karoo, the Cape and the Drakensberg, reaching over 3,480m. Here ancient or conservative mammals, such as golden-moles, blesmols and the Cape Grysbok, occupy the vestiges of a temperate region that has slowly shrunk as Africa migrated north.

Africa's links with Eurasia have pivoted on relatively brief periods of connection. Sometimes the land masses touched at the south end of the Red Sea, but mostly it has been in the north, at Suez. The land bridges between Morocco and Spain, across the Straits of Gibraltar, and between Tunisia and Italy over the Straits of Sicily, appear to have been less influential for mammals, but the Gibraltar connection is known to have been narrow but solid at about 5.5 mya.

At least five periods of connection, during which significant exchanges of fauna and flora took place, occurred between 23 mya and the present. The better-known emigrants were African apes, monkeys and elephants, while early ungulates, hares, a succession of Eurasian rodents and carnivores were immigrants. Altitude, latitude, natural barriers and soils all influence mammals in ways that are touched upon in the profiles of species.

CLIMATE

Africa is a relatively dry continent and its rain derives from evaporation off seas that warm and cool with the seasons and with ocean currents. Wind and rain cycles are set in motion by temperature differences over land and sea, so northern and southern hemispheres have single seasons while the equatorial belt enjoys two wet seasons.

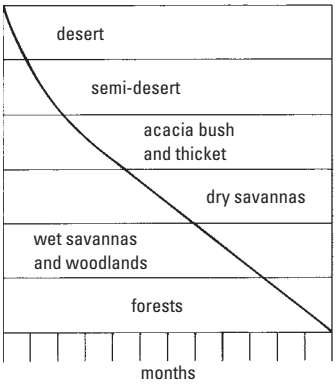
Because cooler conditions bring less evaporation, Africa is dry north of the Equator during the northern winter and dry to the south in the southern winter. In the subtropics, conditions are hotter than in temperate latitudes and drier than in equatorial ones. The mountains have their own climatic pattern, with marked temperature extremes between day and night, heavy rainfall, especially in the equatorial and tropical belts, and generally cooler temperatures overall. The Cape and Mediterranean littorals have different patterns of dry summers and wet winters.

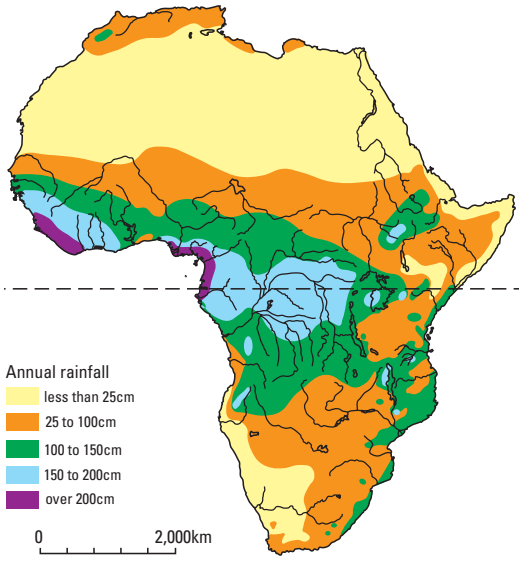
Excluding the Equator, coastal strips and mountains are the main beneficiaries of rain coming in off the Atlantic and Indian Oceans, and heavy rains in all tropical uplands create long river systems that often flow across otherwise arid lands. The archetypal river of this sort is the Nile, but many less well-known rivers show a similar pattern. A worrying trend of hijacking source-waters of rivers, great and small, to irrigate agribusiness schemes leaves people and animals downstream finding their pastures and water drying out.

Seasons are irregular, especially in the subtropics and in the dry corridor that runs from NE to SW Africa. Droughts are often followed by floods – in shallow basins, such as the Rukwa depression and L. Chad, massive evaporation and empty feeder-streams cause periodic drying up of these lakes with attendant die-offs of large antelope and hippopotamus populations. Very arid hinterlands may have narrow coastal strips where nocturnal fogs are sufficient to support some vegetation. On the Namibian foreshore, the Somali coast, up the Red Sea, and along the Mediterranean and Atlantic coasts, these dew thickets or fog-fed grasses support uniquely adapted plant and animal communities that survive on narrow 'island strips' bounded by sea on one side and true desert on the other (mammal examples comprise several gerbil species tied to north and south Atlantic, and Mediterranean, coastal dunes, a vole on the eastern Libyan littoral, the Silver Dikdik in Somalia and Grant's Golden-mole in Namibia).

The Sahara and Horn of Africa desert areas are part of a much larger zone, stretching to the Himalayas, where dry air subsides and clouds rarely form. Throughout Africa it is drought that inhibits plant growth, not absence of light, nor low temperatures. Snow and frost are regular features only on the very highest mountains and at the temperate extremities of Africa. Surface drinking-water

Rainfall and vegetation: the diagram below correlates the duration of humidity (in months) with vegetation zones. Rainfall exceeding 5cm indicates a humid month.



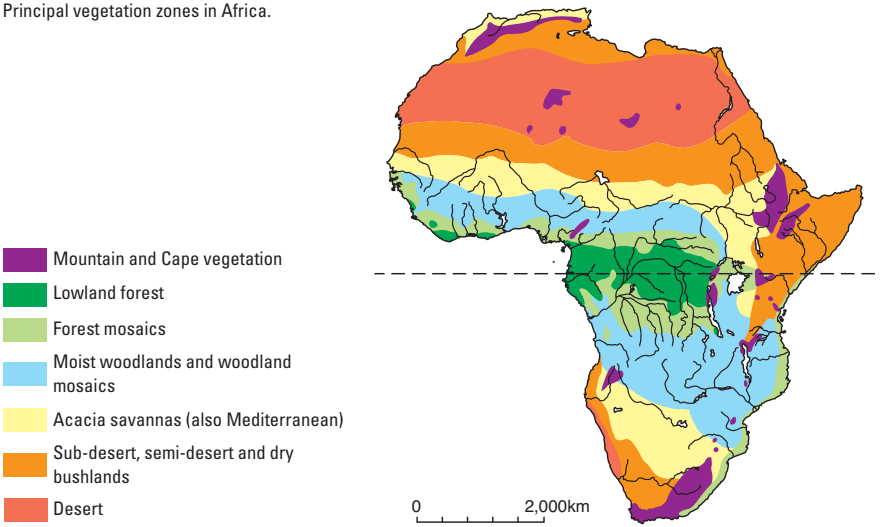


is the single most limiting climatic influence for the majority of mammals, and pastoralists denying wild animals access to waterholes continue to precipitate die-offs over extensive areas. Those species that can extract sufficient moisture from their food alone are the classic desert rodents, some antelopes and some carnivores. It is symptomatic of the short-sightedness and indiscipline of human cultures that all the larger animals best adapted to survive in the Sahara desert have been exterminated. It was said it could not be done, but in less than a century an area larger than the USA has indeed been stripped of all its larger mammals by several generations of ignorant boys playing with guns, fences and vehicles.

VEGETATION

African vegetation is dominated by an equatorial belt of rain-fed forest and three principal desert areas: the Sahara, the Horn (Somalia) and south-west Africa (Namibia). Between these extremes are moist forest–savanna mosaics, woodlands (dominated by leguminous trees, called Miombo in the south-east and Doka in the north-west), various wooded grasslands or savannas, often dominated by *Acacia* bush or scrub, and verging on sub-desert or semi-desert in places. The desert graduates from bare sand dunes (erg) and rocky pavements or screes (hammada) through various conditions in which ephemeral grasses or herbs, scattered shrubs and small trees modify the desert sufficiently to permit various mammals to survive.

Principal vegetation zones in Africa.



Montane areas also range from nearly bare screes on the top of Mt Kilimanjaro through various afroalpine habitats to montane grasslands, moorlands and forests. In the Cape and Karoo there are unique shrublands, moors, grasslands and semi-deserts subject to frequent summer fires and sustained by winter rains. There are few places where these vegetation communities have not been affected by human settlement, felling, frequent fires and large herds of livestock. Nonetheless, Africa's fabled national parks have often succeeded in maintaining relatively healthy and representative communities of indigenous animals and plants.

The gross vegetation zones listed above break down into subtypes that often define the habitats of particular mammal species. Some major types and categories are:

A. FOREST

1. Lowland rainforests (wetter and drier types)
2. Dry evergreen forests
3. Swamp forests (palms, mangroves etc.)
4. Montane forests (afromontane, Mediterranean etc.)
5. Mediterranean oak and conifer forests
6. Various mosaics and transitions

Partially cleared forest, Yekepa District, Liberia. PHOTO: M. COE

Afro-montane rainforest, Parinari mist forest, Mount Nimba, Liberia. PHOTO: M. COE

Forest–savanna transition Pare Mountains, Tanzania. PHOTO: J. KINGDON

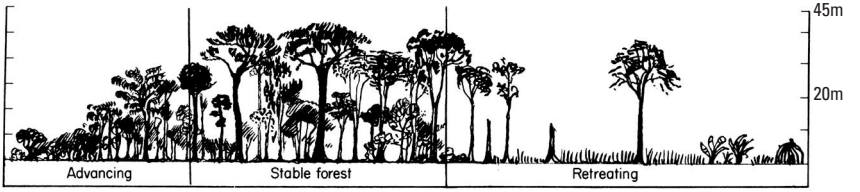


Diagram of forest profile, showing changes in ground cover.

Swamp forest, *Phoenix, Marantocioa, Pseudospondias, Elaeis, Mitragyna, Calamus.*

Montane forest, *Podocarpus, Cyathea, Ocotea, Aningeria.*

B. WOODLANDS

1. Miombo (*Brachystegia*/*Julbernardia* dominant)
2. Sudanian doka (*Isoberlinia* dominant)
3. Mopane (*Colophospermum* dominant)
4. Various mosaics

Mopane woodland, Zimbabwe. PHOTO: M. COE

Woodland, *Brachystegia*, *Terminalia* spp.

C. SAVANNAS, BUSHLANDS AND THICKETS

1. Various *Acacia* dominant (evergreen to very dry)
2. Bushlands and thickets (often *Commiphora* dominant)
3. Mosaics (from moist to very dry)

Open *Acacia* savanna, Nyambeni, Kenya. PHOTO: M. COE

Acacia savanna, *Acacia* spp.

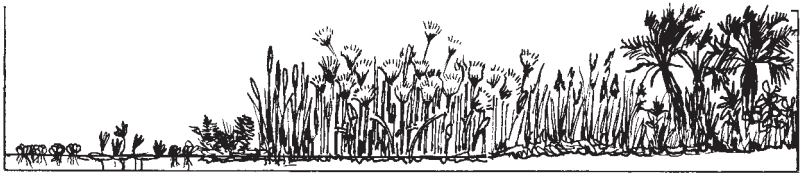
Thicket, *Commiphora*, *Combretum*, *Acacia*, *Teclea*, *Maba*.

Acacia/Commiphora/Combretum thicket, Mkomazi, Tanzania. PHOTO: J. KINGDON

D. GRASSLANDS AND MARSHES

1. Fire-induced grasslands (*Themeda* etc.)
2. Valley bottom grasslands (some semi-aquatic)
3. Montane grasslands
4. Various mosaics and secondary types

Fire-induced grassland, Samburu, Kenya. PHOTO: B. WHITE



Swamp, *Pistia, Nymphaea, Phragmites, Papyrus, Miscanthidium, Phoenix.*

Swamp vegetation, Okavango, Botswana. PHOTO: M. COE

Giant groundsel, Afro-alpine zone, Mount Kenya. PHOTO: M. COE

E. MONTANE AND AFROALPINE

1. High-altitude alpine types
2. Bamboo (plus forest/grassland mosaics)
3. Undifferentiated (from arid to humid)

Juniper–hagenia forest/grassland mosaic, Bale Mountains, Ethiopia. PHOTO: J. KINGDON

Alpine zone, *Lobelia*, *Carex*, *Senecio*.

Subalpine or ericaceous zone, *Erica arborea*.

Bamboo, *Arundinaria*.

F. SHRUB, SCRUB, MOOR AND SEMI-DESERT

1. Semi-arid shrublands
2. Succulent Karoo types
3. Cape fynbos
4. Desert margins scrub and mosaics

Cape fynbos. PHOTO: J. KINGDON

G. DESERTIC

1. Absolute desert
2. Sand deserts (ergs)
3. Stone deserts (hammada, reg)
4. Sub-deserts (graded or mosaic)
5. Semi-deserts (graded or mosaic)

Subdesert, Namaqualand, South Africa. PHOTO: M. COE

Semi-desert, *Aloe*, *Calotropis*, *Sansevieria*, *Commiphora*, *Balanites*, *Euphorbia*.

MAMMALIA MAMMALS

ORDER 1: Hyraxes
ORDER 2: Proboscids
ORDER 3: Sea-cows (Sirenians)
ORDER 4: Afrosoricids
ORDER 5: Sengis (Elephant-shrews)
ORDER 6: Aardvark
ORDER 7: Primates
ORDER 8: Rodents
ORDER 9: Hares
ORDER 10: Hedgehogs
ORDER 11: Shrews
ORDER 12: Bats
ORDER 13: Carnivores
ORDER 14: Pangolins
ORDER 15: Odd-toed Ungulates
ORDER 16: Cetartiodactyls

Every user of this book is a mammal and, as doctors, physiologists and other scientists have always known, the study of human kinship with other mammals offers us many fundamental truths about ourselves. Take warm blood for example. Internally stable temperatures are central to what mammals are. A naked human freezes to death within hours in a northern winter and, likewise, quickly dies of heatstroke if exposed to a desert midsummer. This is because *biologically* we are still fragile equatorial primates. While we have developed technical solutions to both these extremes of climate (i.e. clothes or air conditioners), other mammals have biological techniques that enable them to survive both extremes, relying on fur for insulation against extremes of temperature, and sweating or panting in order to cool down.

It is glands similar to sweat glands, mammae, which have been modified to produce milk, that give mammals both their common and their scientific name – mammals are animals whose mothers have mammary glands.

Mammal mothers are unique not only in nursing their offspring on milk but in nurturing them *before* birth through a placenta that grows into the wall of the uterus. The placenta allows the foetus to plug into its mother's circulation and so share in her respiratory and excretory systems and in the nutrients carried in her blood. It also stops the mother rejecting the foetus as an alien body.

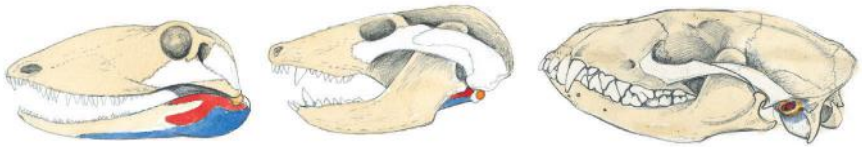
A mammal is not only sheltered as a foetus in the womb, maternal care also shelters it after birth. Whereas emergence from an egg exposes a newly hatched invertebrate, fish or reptile to predators, competitors, changes in climate and the need to find food, newborn mammals escape these rigours through maternal care. Mammals are also relatively independent of the environment for the duration of their infancy and adolescence. This trait is unique to mammals and is most prolonged in primates, especially hominid apes. Among hominids, humans have extended this central mammalian characteristic furthest. Not only has our childhood been extended biologically, contemporary humans continue to extend its environmental dimension – detachment from ecological systems. Because much of our technology plays a role analogous to maternal protection we have, in a limited sense, become permanent youngsters, the most mammalian of mammals.

Mothering is also the key to social life in mammals. The physical costs of bearing and suckling offspring are so great for the females that they go to elaborate lengths to fit the timing of reproduction to the best time of year and to ensure access to the best resources both for themselves and for their offspring. To achieve this some species share or enter the territories of prime male land-holders. Others seek out the protection of dominant males at the top of a strict hierarchy while still others choose males that will help raise offspring.

Different patterns of male competition and female choice have dramatic consequences for the external appearance and anatomy of males. Weaponry, in the form of horns, tusks or antlers, has been developed to defend territories or rank. Age-graded gigantism has evolved in the males of hierarchical species, such as gorillas, elands and Giraffes. Long-term pair-bonding is usually matched by the sexes being of similar size (typified by African Wild Dogs).

Diversity of size and form is built on those most fundamental of faculties: finding and processing food. Major groupings within the mammals are often named and defined by the shape and form of their teeth (such as rodents, scandents, tubulidents). Furthermore, mammals as a whole have uniquely modifiable teeth and lower jaws. Although these derive from structures similar to those in other vertebrates, the jaw consists of a single mandibular bone anchored in and powerfully hinged onto the skull. Reptiles, by contrast, have jaws that are a weaker assemblage of bones.

Long series of fossils of the now-extinct 'mammal-like reptiles', or synapsids, have revealed that the tooth-bearing bone (the reptilian 'dentary') first developed a hinge with the squamosal, or cheekbone, about 200 million years ago. As a consequence, three of the original reptilian jaw bones (themselves derived from fish gill-arches) declined in size and became detached from the lower jaw. However, these diminutive bones did not become redundant but attached themselves to the skull base, where they became the inner components of the mammal ear capsule. Partly because of the fine tuning of these minute bones mammals have developed a much more discriminating sense of hearing than reptiles and have elaborated numerous forms of sonic communication, sonar orientation and detection systems. Thus mammals owe their good ear for the nuances of sound to their peculiar legacy from a reptile-like anatomy.



Transformations through time. Synapsid (mammal-like reptile) skulls: *left*, *Ophiacodon* (an early form); *centre*, *Probainognathus* (a later form) compared with a modern mammal, the civet, *right*.

The senses play a very precise role in the life of all mammals. Sight, hearing, scent and touch are balanced in permutations that are unique to each species, and that balance finds a gross expression in the shape of animal heads. For example, a Serval's huge ears, a fishing genet's moustache of face whiskers, a galago's bulging eyes and an Aardvark's nose tube each manifest unique techniques for finding food. All possess a full set of faculties but the Serval must pick up sound waves from mice in dense grass, the genet senses waves from small fish in water, the galago

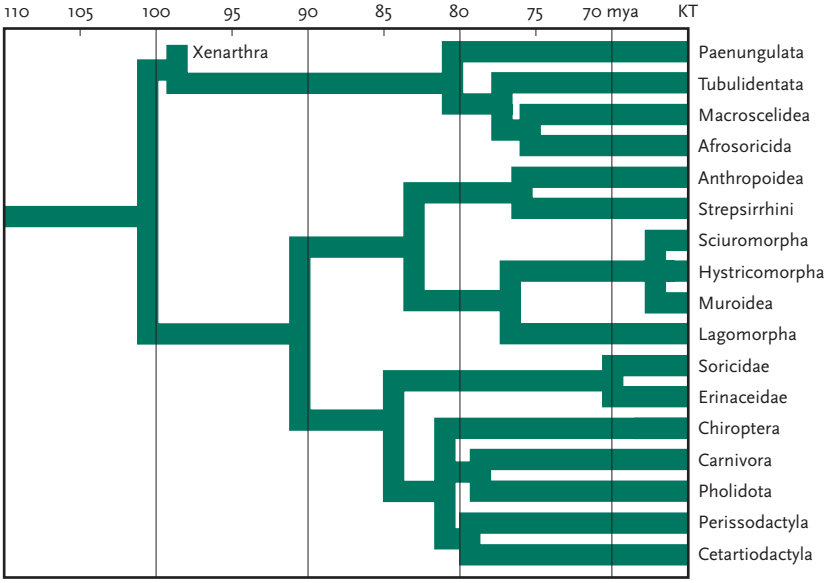
Mammal heads and senses: (a) Serval (hearing); (b) Fishing genet (touch); (c) Galago (vision); (d) Aardvark (hearing).

receives optical wavelengths in near total darkness and the Aardvark locks onto molecular traces of scent emanating from termites hidden deep in the soil. All these faculties had to be developed by stages from the less specialised conditions that preceded them.

The overall shape and proportions of a mammal are therefore the end-products of its lineage and its progressive adaptation to an exact and exacting ecological niche. Much of the fascination of observing animals lies in matching such expressions of form to function. Form is not only anatomical; mammals act, behave, occupy habitats and have habits that are all expressions of their total adaptation. Every species manifests a unique way of making a living.

Much of that life is accessible to quiet observation but any serious contemplation of mammals can only be a humbling experience. In their world we are like deaf-mutes. We can neither register nor interpret the most important dimension of their existence: scent. For a few species (mostly primates like us) scent may be subordinate to vision but for the majority scent is a central regulator of their social life, a major mechanism for orienting themselves and a source of what we would call 'exquisite sensations'.

If mammals have been shaped by the way they make a living, they also shape the lives of their prey and of the plants they eat. An example is my own discovery of a unique relationship between bark-eating anomalures and the awoura (*Julbernardia*) trees on which they feed (see p.250). This interdependence between gigantic, slow-growing forest trees and small, short-lived, gliding rodents is so specific that it must go back millions of years. In keeping their flight paths to the tree trunks clear, the anomalures prune (and eventually kill) the tree's competitors, thereby compensating them for wounding their bark. Mutually beneficial relationships are known among bats and the flowering plants that they pollinate, and among primates and the tree seeds that they disperse, but many, much subtler relationships await discovery and study. The inter-relatedness of mammals and all other organisms in natural communities is a compelling reason why we should strive to conserve ecosystems intact, as well as the entire range of mammal species, not just the ones we find attractive or agreeable.



Tentatively dated molecular tree for mammalian radiation before the KT event (65.5 mya) (after Meredith *et al.* 2011).

During the nearly 20 years since the first edition of this guide was written and published, an entirely new supercohort of mammals has been recognised. We owe this recognition to the science of molecular phylogeny, which has clarified relationships within and among virtually all mammal groups through detailed comparison of their genetic profiles. About 80 species of extant afrotheres are currently recognised, these include three elephants (two of which are African species), four sea-cows (two African), nine hyraxes, one aardvark, 18 sengis (elephant-shrews) and 21 golden-moles (all African) and three otter-shrews, which have some still poorly understood affinity with Madagascan tenrecs.

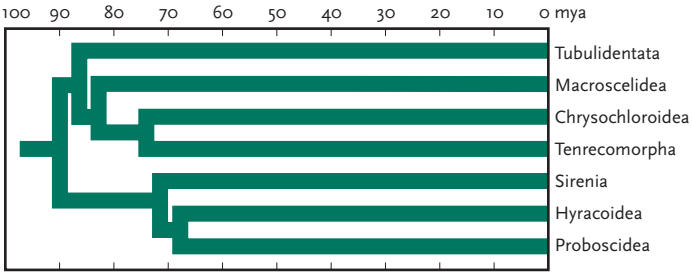
The afrothere radiation in Africa is tied in to the central question of just where modern placental mammals arose. Are these animals modern derivatives of the very earliest placental mammals or are they a later product of a chance over-sea rafting during the continental isolation of Afro-Arabia? If the Afro-Arabian continent was as decisively isolated as is currently thought, its placental afrotherian colonist must have had some tolerance for exposure at sea. Whether this implies semi-aquatic habits remains a conjecture. Both placental mammal and afrotherian origins continue to be matters of ongoing debate. Nonetheless, the reality of Afrotheria is but part of a global effort to construct genealogical trees for all biota – ultimately the single Tree of Life. Several mammal lineages from outside Africa and members of the Afrotheria share many similar or convergent adaptations, such as ant-eaters with sengis, large-scale aquatic whale and hippo-like mammals resembling afrotherian sea-cows and, on a miniature scale, true shrew-like moles converging with afrotherian golden-moles.

The oldest, undisputed members of afrotherian orders appear as fossils in north-west Africa. No other group of placental mammals is known to have existed in Africa before the Afrotheria and they represent a continuous presence for at least 65 million years and perhaps as much as 90 million years. Outrageously, but also sadly, environmental and biological ignorance among contemporary policy-makers, economists and 'developers' renders them indifferent to the survival of Africa's fauna, including Afrotheria, our most ancient indigenous mammals.

PAENUNGULATA

The six orders of Afrotheria have been divided, quite recently, into two cohorts: elephants, sea-cows and hyraxes comprise Paenungulata, while the new cohort, Afroinsectiphillia, embraces the Aardvark, sengis, otter-shrews and golden-moles. Vast differences among its members would make their common grouping scarcely credible until we learn how long ago the lineages are thought to have diverged – paenungulates and afroinsectiphillians between 90 and 80 mya while ancestral elephants and sea-cows, now superspecialised, diverged from the more typically mammalian hyraxes some 75–65 mya.

Compared with other placental radiations, paenungulate species are very few. Extant species are also highly specialised, which reflects a long head-start in adapting to difficult niches. The low diversity of surviving species, notably elephants and sea-cows, has been influenced by human predation. There is evidence for prehistoric and historic humans exterminating at least 10 species. This guide begins with hyraxes, as the least derived of all afrotheres.



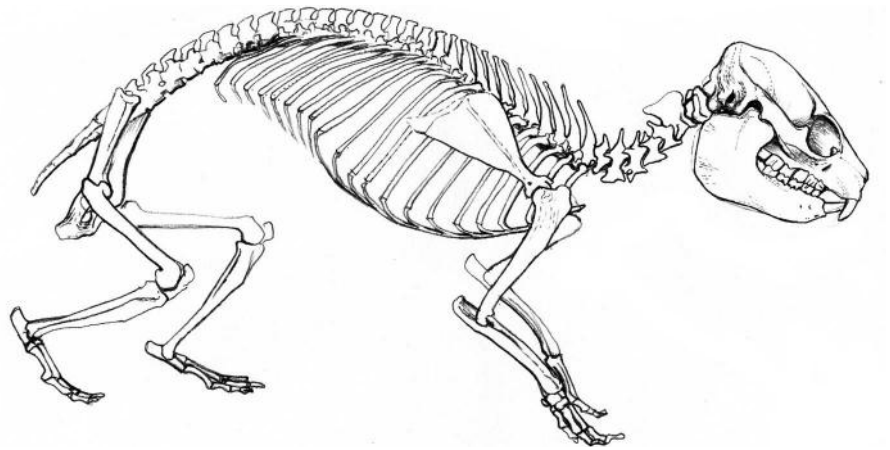
Tentative phylogenetic relationships of afrotherian mammals based on analysis of genomic data (after Meredith *et al.* 2011).

HYRAXES HYRACOIDEA

Hyraxes are small, woolly animals with no visible tail and blunt digits. Vernacular names such as 'rock rabbit', 'coney' and 'dassie' ('little badger') illustrate traditional uncertainties about what sort of animal they are, and they still tend to be likened to guinea-pigs or groundhogs! It was that exceptionally perceptive anatomist Thomas H. Huxley who first put them into an order of their own and this has been followed up to the present. At least 20 genera of hyracoids are known from Africa, many from the Oligocene, some 30–25 mya, at which time some were dominant herbivore species. They have been almost totally replaced by modern ruminants but the reasons for the hyraxes' decline probably has less to do with their digestion (which, judging from modern hyraxes, was probably hardly less efficient than that of ungulates) than in a poor ability to regulate body temperature, a lack of stamina, short legs and a primitive brain that still shows resemblances to those of 50-million-year-old 'near ungulates'. Other limitations could be slow reproduction and their cumbersome, though fast, way of cropping vegetation. The tusk-like incisors of hyraxes are given over to defence and grooming, which has forced the molars and rear of the mouth to combine the functions of food-gathering and chewing.

Hyraxes were first classified with elephants because early fossils of both lineages were similar. That several ancestors had much larger body sizes might be relevant to understanding their 7-month gestation and the very advanced state of development of the newborn. More immediate ancestors of modern hyraxes are likely to have escaped competition from bovids of Eurasian origin by adapting to the rocky thickets that are scattered over a large part of Africa. If rock-dwelling was the initial innovation of the ancestors of all living hyraxes, the two specialisations that have developed since are arboreal skills at one extreme and grass-eating at the other. The Bush Hyrax has the most generalised dentition.

All three genera are successful and they flourish in two environments that hoofed ungulates cannot cope with: trees and rock piles.



Skeleton of *Procavia capensis*.

HYRAXES PROCAVIIDAE

Rock hyraxes	*Procavia* (5 species)
Bush Hyrax	*Heterohyrax brucei*
Tree hyraxes	*Dendrohyrax* (3 species)

The three genera of hyraxes show few easily observable external differences: all are rabbit-sized, woolly and brown, with a large-mouthed, deep-jawed head and rubbery, blunt-fingered hands and feet. Their loud voices are highly distinctive and their calls are currently the subject of systematic analysis.

Although skulls and teeth remain the most reliable guides to genera, each occupies a different niche with a distinct diet. Rock hyraxes are mainly diurnal, arid-adapted grazers, living in colonies among rocks. Tree hyraxes are mainly nocturnal browsers, scattered singly or in small groups among moist forest trees. Bush Hyraxes are diurnal browsers that feed in trees but live in colonies among rocks.

All species have very long bodies that are concealed by a hunched posture and long fur. All have long, tactile hairs, especially on the muzzle, throat, brows, cheeks, rump and limb joints. All species have skin glands that run down the spine and most have differently coloured hair patches that can be erected or fanned open as scent-dispensers. Both identity and status are signalled by scent. Disproportionately large jaws and an ability to draw the lips right back allow them to bite off and chew large mouthfuls of vegetation at a time. This means that two or more short feeding bouts are sufficient to fill the stomach.

Long periods of inactivity (in carefully chosen sites and sometimes lasting several days) both conserve energy and also help digestion. Hyraxes can weather extended droughts in the absence of water and on diets of very low nutritive value. Both gut and kidneys are highly efficient at extracting nutrients and saving water. Urine is copious and dilute in the wet season but very concentrated and syrupy in the dry season. Several species urinate at communal 'latrines' that may be centuries (or millennia) old. All species drop their dung at specific spots. Dung, urine and very loud calls (amplified by guttural pouches) are used to define territories. These may be effectively group territories but are primarily defended by single adult males. The male's home range is shared by one or more females and their offspring. The age at which young males are expelled varies. They disperse into peripheral ranges, there to develop or await tenancy of their own territories in a very vulnerable situation.

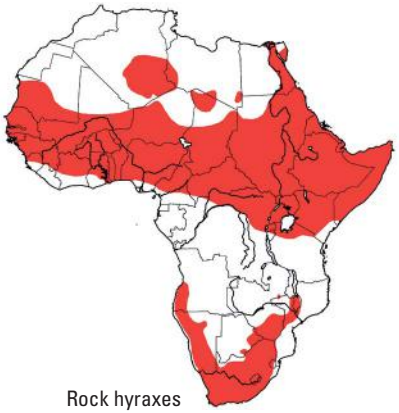
Low-level aggression underpins much of the hyrax's social life. Dominance is indicated by bristling fur, an exposed dorsal gland, tooth-grinding, snapping and growling. Upper incisors are very sharp and can inflict deep and damaging bites. Appeasement gestures are therefore pervasive, especially 'presenting' of the rump with fur and body as flat as possible. This may help explain why hyraxes typically enter holes, huddle in groups, and even brawl, facing backwards.

The genera differ substantially in their mating calls and genital structures. Most species are seasonal breeders. In males the weight of the testes increases by up to 20 times, with corresponding surges in testosterone and male aggression. A gestation of 7 or 8 months is almost without precedent in such a small animal but the infant is born fully developed and takes its first nibble of plants within 4 days. Young are weaned by 3 months and are sexually mature by 16 months. They are known to live for up to 12 years.

In addition to persecution from humans, hyraxes suffer predation from numerous carnivores and raptors, especially cats, jackals, eagles (most notably a hyrax-eating specialist, Verreaux's Eagle) and eagle-owls.

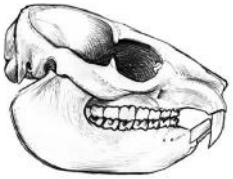
Rock hyraxes (*Procavia*): Tooth-row tapered and bowed, with broad and deep teeth. Row of four front teeth shorter than that of the three back teeth. Attachments for temporal chewing muscles converge on midline of domed braincase. Advertising call is a long series of ascending yelps descending to grunts.
Bush Hyrax (*Heterohyrax*): Cheek-teeth intermediate but sharply cusped. Row of four front teeth about equal to that of the three back teeth. Attachments for temporal muscles meet or nearly meet on top of curved braincase. Advertising call is a penetrating series of whining mews.
Tree hyraxes (*Dendrohyrax*): Cheek-teeth narrow, relatively shallow, sharply cusped. Row of four front teeth longer than that of the three back teeth. Attachments for temporal muscles widely separate on sides of flat braincase. Advertising calls are very variable but all have ascending cries and very loud crescendo.

Ethiopian Rock Hyrax



Rock hyraxes

Black-necked Rock Hyrax



Black-necked Rock Hyrax

ROCK HYRAXES *Procavia*

Five forms, treated here as full species (see below)

OTHER NAMES Klipdassie. Fr. *Daman de rocher*. Ger. *Klippschliefer*. Swah. *Pimbe mawe*.

MEASUREMENTS HB 380–600mm. W 1.8–5.5kg.

RECOGNITION Blunt-faced hyraxes that vary in colour both regionally and individually but generally brown with a paler underside.

GEOGRAPHIC VARIATION Sometimes treated as a single species, *Procavia* has also been divided into five species, some still further subdivided into subspecies. Dorsal patches can be yellow, black or piebald in the two most central populations but outlying species are more consistent in the colour of their patches.

Cape Rock Hyrax, *P. capensis* (S and SW Africa): black dorsal patch; **Ethiopian Rock Hyrax**, *P. habessinica* (NE Africa and Arabia): variable dorsal patch; **Black-necked Rock Hyrax**, *P. johnstoni* (central and E Africa): variable dorsal patch; **Kaokoveld Rock Hyrax**, *P. welwitchii* (Kaokoveld): pale cream dorsal patch; **Red-headed Rock Hyrax**, *P. ruficeps* (S Sahara): orange dorsal patch.

DISTRIBUTION Drier rocky areas of Africa and Arabia.

HABITAT Mainly rock outcroppings, often in areas where the rocks themselves assist the growth of vegetation by trapping moisture or nutrients. Rocks also create micro-climates that can be cooler, warmer, drier, moister, more shady, sunnier or less windy than the surroundings. Hyraxes can therefore counteract climatic extremes to some extent by finding surfaces or crevices that suit their physiological needs at any particular time. Crevices also provide shelter from predators.

FOOD Mainly grasses and herbs grazed within easy reach of shelter. Common grasses taken are species of *Aristida*, *Chrysopogon*, *Tetrapogon* and *Latipes*. In the alpine region of Mt Kenya *Festuca* is a staple. Shrubs and trees are also climbed and browsed, sometimes only seasonally. Feeding is limited to about 1 hour in the early morning and a longer session in late afternoon. Animals may feed at night during desert summers.

BEHAVIOUR Territorial, with single male territories containing various numbers of females and their offspring, up to a total of about 25 animals. In an outcrop the number of territories depends partly on their individual defendability but mainly on their year-round resources of food and shelter. Females are generally closely related and frequently come into close physical contact with other females and young within their unit. However, adult females have their own exclusive core areas, albeit ones that are very close to their fellows. There is no very marked hierarchy other than the territorial male's position of dominance. His intolerance of maturing male offspring leads to an

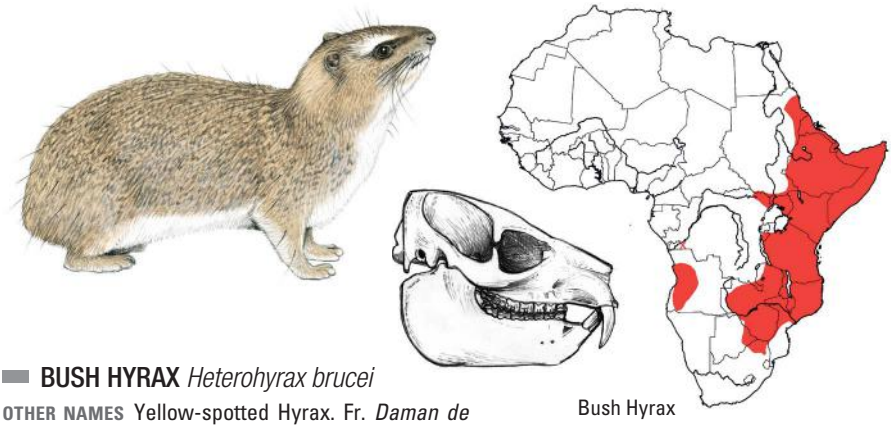
emigration and selective exposure of young males, which leads to an imbalance of the sexes, especially among adults.

All members of a single territorial group or colony share a number of latrines. These appear to be of two types. Urine is dribbled down very exposed, outward-facing rocks where calcium carbonates dissolve and are deposited as very conspicuous white or light-coloured streaks. These may serve as external olfactory and visual markers for specific colonies. The second type of latrine is situated in more shaded, protected sites. Both dung and urine are dropped in the same place, preferably on a flat or nearly flat surface. Here liquids and solids congeal slowly, there is less evaporation and the smell can be very strong indeed. These latrines appear to function as scenting parlours where all members of the group come to share a common smell that scents their feet and fur.

Breeding seasons are often very local and can differ from the top to the bottom of an escarpment. The male is very vocal during the mating season and shakes his head while approaching the female, his dorsal gland open and actively exuding scent. Up to six young are born after a gestation of 214–240 days. Almost immediately active, and soon eating plants, young frequently climb onto their mother's back where they may become scented by her dorsal gland and warmed by her body.

ADAPTATIONS Main speciality is ability to live off coarse desert grasses. Both teeth and digestion differ substantially from arboreal, folivorous species. Conservative in being weaker and less agile climbers.

STATUS Although subject to periodic epidemics, heavy natural predation and very localised depletion or extermination, all major populations of *Procavia* are still numerous.



Bush Hyrax

BUSH HYRAX *Heterohyrax brucei*

OTHER NAMES Yellow-spotted Hyrax. Fr. *Daman de steppe*. Ger. *Buschschliefer*. Swah. *Perere mawe*.

MEASUREMENTS HB 320–570mm. W 2.0–3.5kg.

RECOGNITION A relatively small hyrax with conspicuous pale 'eyebrows', a white or off-white underside and a greyish, pepper-and-salt agouti body colour on some but not all regional variants, with a yellow dorsal spot. Snout more pointed than that of the rock hyraxes; altogether more lightly built.

GEOGRAPHIC VARIATION More than 20 subspecies described, based on variation in coat colour, but many may not hold up to taxonomic scrutiny. Genus formerly thought to include two further species: *H. antinae*, which is a form of *Procavia*, and '*H. chapini*', from the mouth of the Congo R., which probably represents a variant of the dark, thickly-furred Angolan race, *H. b. bocagei*.

DISTRIBUTION Eastern half of Africa and Sinai with extensive outlier in Angola. Includes higher altitudes (notably around north end of L. Malawi/L. Nyasa).

HABITAT Wooded localities on river banks, escarpments and rock outcrops. Normally shelters in rocks but may resort to trees, termitaries or old burrows. Often found in joint colonies with rock hyraxes.

FOOD Leaves, fruits, stems, twigs and bark. On Serengeti outcrops virtually the entire diet comes from two trees, *Acacia tortilis* and *Allophylus*. Acacias are a major food over most of the species' range.

BEHAVIOUR Single colonies can number up to 34 individuals with females mixing very readily with each other and also, where present, with female rock hyraxes. They utter sustained 5-minute bouts

Sketches of Bush Hyrax. Note the erectile fur tract above the dorsal gland.

of loud calls, a whining croak that is much less resonant and deep than that of other hyraxes. Their very bird-like alarm whistle alerts other species, including rock hyraxes and Klipspringers. They flag their heads with a pronounced shiver.

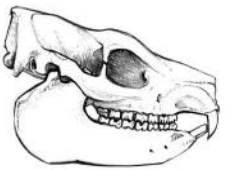
ADAPTATIONS The Bush Hyrax appears to illustrate the earliest steps in the colonisation of trees by an animal apparently ill-equipped to do so. Their primary asset in this niche is probably their exceptionally efficient gut, capable of digesting difficult plant foods.

STATUS Widespread and extremely abundant in many localities.

TREE HYRAXES *Dendrohyrax*

Eastern Tree Hyrax	*Dendrohyrax validus*
Southern Tree Hyrax	*Dendrohyrax arboreus*
Western Tree Hyrax	*Dendrohyrax dorsalis*

EASTERN TREE HYRAX *Dendrohyrax validus*



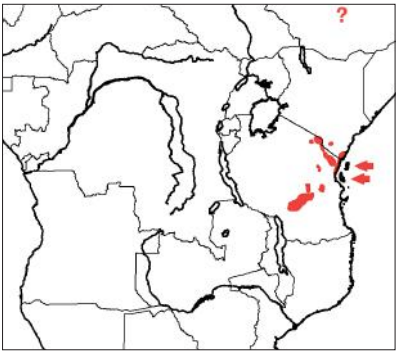
OTHER NAMES Fr. *Daman d'arbre*. Ger. *Ostlicher Waldschliefer*. Swah. *M'ha*, *Perere ya miti*.

MEASUREMENTS HB 470–580mm. W 2.5–3.0kg.

RECOGNITION Variable colouring, mostly warm dark brown to greyish with off-white to cinnamon undersides. Dorsal spot 20–40mm long, russet-coloured.

GEOGRAPHIC VARIATION Possibly represents more than one species. *D. v. validus* (Mt Meru and Mt Kilimanjaro), *D. v. terricola* (Taita Hills, Usambara and Pare Mts), *D. v. schusteri* (Uluguru and Udzungwa Mts – latter may be a distinct form), *D. v. neumanni* (Zanzibar, Pemba and Tumbatu Islands), *D. v.* sp./ssp. nov.? (Ethiopian highlands).

DISTRIBUTION Eastern Arc Mts also Zanzibar and Pemba Is. Ranges from sea level to 3,000m. Sharing the same mainland region, the Eastern Tree Hyrax is restricted to mountains while the Southern Tree Hyrax dominates the lowlands. This suggests a relict distribution partly determined by competition arising from the spread of a more recently evolved species.



Eastern Tree Hyrax

HABITAT Montane forests on the mainland 1,700–3,070m (Kilimanjaro) and lowland forests on the islands. This species used to be particularly common in the higher reaches of montane forest where an impoverished flora grows on leached substrates.

FOOD Predominantly an arboreal leaf-eater but also eats herbs and climbers. Feeding peaks at

dusk and dawn. At the top of its altitudinal range in the Udzungwa Mts, this species lives at very high densities in low canopy mist forest where a very rare and localised species of African violet, *Saintpaulia grotei*, grows abundantly, often rooted in decayed hyrax faeces. These violets seem to escape the heavy browsing of hyraxes in this habitat, suggesting that the herb is distasteful to them. *S. grotei* seems to derive competitive, as well as nutritional advantages from its association with the hyraxes, suggesting that herb and herbivore might have co-evolved.

BEHAVIOUR Generally solitary but densities in the upper Udzungwa Mts (notably on the Gologolo crest) appeared to be very high in 2001, with at least 17 per ha estimated (from frequency and distribution of calls). Calling peaks just after dusk and before dawn and the frequency of calls has been reported to show little change over a period of 8 months. A common pattern consists of bursts of short hacks, sometimes building up to a crescendo of what have been called 'ping-pong' sequences for their resemblance to the sharp crack of a bouncing ping-pong ball. Very loud screams are common in areas of higher density. In the Pare Mts local Eastern Tree Hyraxes make what appears to be a contact call in the timbre of a man's voice asking 'whatsit?' In the Udzungwa Mts middens of faeces and urine can spread over several square metres and cover trunks and the surrounding ground with a very strong-smelling, thick, tarmac-like coat. Animals contributing to this olfactory beacon or 'scenting parlour' clearly acquire a group scent. It is likely that such sites serve to identify local 'clans' and that social behaviour may turn out to be complex and mediated by both sound, scent and physical contact. Gestation is about 7.5 months and births peak on Kilimanjaro in August.

STATUS Eastern Tree Hyraxes are at risk from felling and firing forests on Pemba and Zanzibar Is. In the mountains, hunting and logging are the most immediate threat. Lack of research into the basic biology and ecological needs of this species is regrettable because their uneven abundance and patchy distribution will need to be understood before practical conservation plans can be attempted. The state of local and distinctive populations of the Eastern species need attention and a yet-to-be described form of tree hyrax from forest relicts in Ethiopia is a particular cause for concern.

SOUTHERN TREE HYRAX

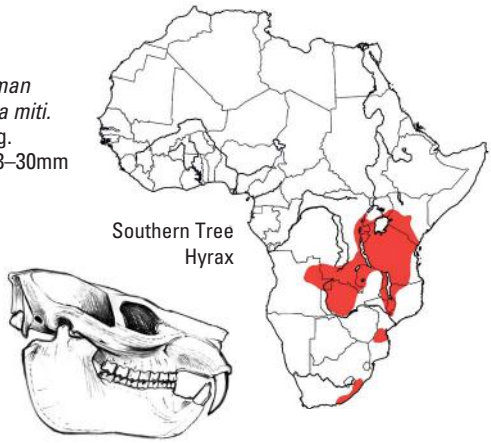
Dendrohyrax arboreus

OTHER NAMES Southern Tree Dassie. Fr. *Daman d'arbre*. Ger. *Waldschliefer*. Swah. *Perere ya miti*.

MEASUREMENTS HB 440–560mm. W 1.2–2.6kg.

RECOGNITION Soft-furred, dorsal patch 23–30mm long and cream-coloured.

GEOGRAPHIC VARIATION *D. a. arboreus* (Eastern Cape, KwaZulu-Natal and central Mozambique), *D. a. braueri* (Eastern Angola to L. Tanganyika and Zambezi R.), *D. a. mimus* (vicinity of L. Malawi/Nyasa), *D. a. stuhlmanni* (Tanzania and vicinity of L. Victoria), *D. a bettoni* and *D. a. crawshayi* (Kenya), *D. a. adolfi-frederici* and *D. a. ruwenzorii* (high mountains of central Africa).



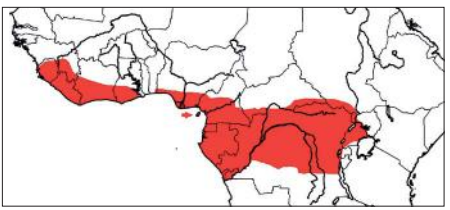
DISTRIBUTION Eastern, southern and south-central Africa in a somewhat scattered range as far as the eastern Cape.

HABITAT Forests, moist savannas, evergreen thickets and mosaics (derived from forest) and montane habitats. *D. arboreus ruwenzorii* and related forms are (or were) abundant throughout the afroalpine and forest zones of W Uganda and E DR Congo. On the higher reaches of these cold, wet mountains the hyraxes live among rocks, are partly diurnal and have colonial habits. In montane forest they are arboreal, nocturnal and tend to be more solitary.

FOOD Leaves, fruits and twigs in the canopy, grasses and sedges on screes. Giant groundsel and numerous aromatic leaves and herbs are regularly eaten. Rapid feeders, these animals can eat a third of their own body-weight of food in a day.
BEHAVIOUR In the Rwenzori and other high mountains of central Africa these hyraxes can live at very high densities. Elsewhere they tend to be more scattered. They are territorial and very aggressive during the mating season. Both males and females exude secretion from their dorsal glands at this time. Male courtship involves following the female, calling and gland-fanning with penile erection. Gestation is about 8 months, with the precocious 400g newborn able to climb on its first day.
ADAPTATIONS As with all tree hyraxes, the most obvious speciality is contortionist mobility in their relatively long limbs and body. Mainly nocturnal habits may have stimulated the extraordinary volume, variety and frequency of their calls. Loud advertising or territorial calls are particularly variable, even within one species and from one side of a big river to another. All loud calls involve long series of cries that gradually grow louder, climaxing in barks, shrieks or choking screams. Extreme volubility in tree hyraxes is sometimes seasonal and can begin well before dark and continue all night during peak periods and in areas of high density.
STATUS Southern Tree Hyraxes could be at risk from clear-felling in some localities, from snaring in others. Snaring for meat and skins is also severe in many central African mountains.

WESTERN TREE HYRAX *Dendrohyrax dorsalis*

OTHER NAMES Fr. *Daman d'arbre*. Ger. *Waldschliefer*. Swah. *Maparaka*, *Perere miti*.
MEASUREMENTS HB 440–570mm. W 1.8–4.5kg.
RECOGNITION Very coarsely furred, dark brown to black (although pale, cream-coloured morphs are also known). Tends to be softer-furred in the lowland forests of Uganda, probably a consequence of long-term hybridisation with the Southern species, *D. arboreus*.
GEOGRAPHIC VARIATION Fifteen supposed subspecies have been named. So far there is no basis for assessing the validity of any of them.
DISTRIBUTION An equatorial species from both sides of the Congo R. Known from the Scarcies R. in Upper Guinea to the Nile R. in Uganda. The Western Tree Hyrax is a lowland forest species that has reached the Nile leaving populations of the Southern species isolated in the higher reaches of central African mountains.
HABITAT Lowland rainforest but also in degraded patches within cultivated savanna mosaics.
FOOD Nocturnal browser of leaves, shoots, twigs and fruits in the canopy but occasionally forages on the forest floor.
BEHAVIOUR Little known but generally thought to be solitary and territorial. Gestation is about 8 months and young can reach adult size between 120 and 200 days.
ADAPTATIONS Possibly the most adept climber among all tree hyraxes, possessing an exceptionally strong, firm grip with all four feet. Both sexes utter very loud, long cries that gradually grow louder, repeated 22–42 times and climaxing in an eerie shrieking crescendo. Calling frequency varies seasonally and with peaks between 20.00 and 22.00 and 04.00 and 05.00 hours. They have been heard to stutter, snap their teeth and salivate when excited.
STATUS Widespread and not endangered overall but a sudden increase of hyraxes on market stalls on Bioko Is. suggested hunters had discovered new techniques for catching them.

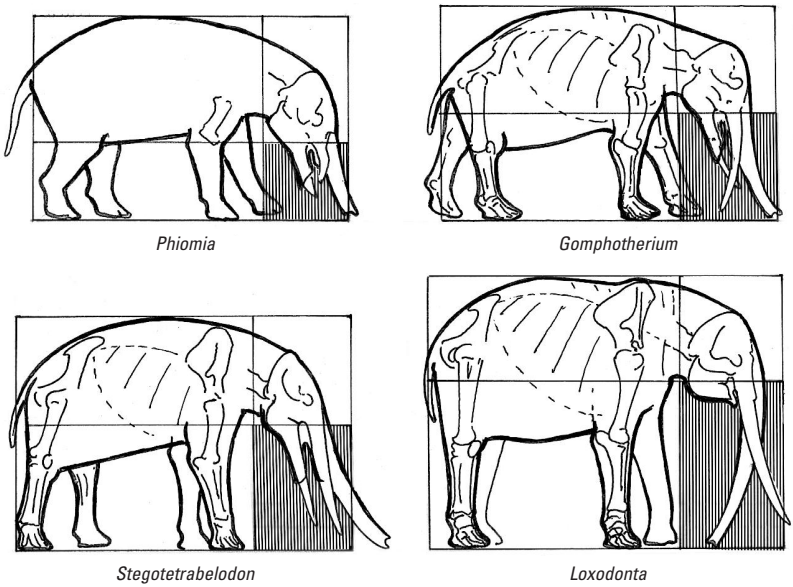


Western Tree Hyrax

PROBOSCIDS PROBOSCIDEA

The proboscis or trunk is thought to have been the primary structure that made possible the evolution of elephants' great size, height and long tusks. Trunks are capable of powerful twisting and coiling while gathering food or wrestling with other elephants but can also perform delicate movements, such as picking berries, rubbing eyes or exploring orifices. Trunks can draw up columns of water or dust, and their great length can reach up to 7m or burrow down into sand, soil or crevices to reach deeply hidden water. While the development of a trunk relieved the incisor teeth of most of their feeding functions, the incisors' potential as weapons developed rapidly as the elephants' ancestors increased in size. As they evolved bigger and bigger bodies, elephants lost versatility in their limbs, which, first and foremost, had to bear great weight. Physical contacts with fellow elephants and with the environment became focused on the head: the trunk handled food and gentler forms of social contact; tusks became both tools and weapons of defence used in ritualised fighting with their own species.

Elephants fossilise well, so an ever-more detailed picture of later elephant evolution continues to unfold from a wealth of fossils (the earlier stages are less well documented). Before 65 mya elephants had shared a common ancestry with hyraxes. Early elephants and early sea-cows began as wallowing herbivorous cousins but one remained terrestrial while the other became wholly aquatic.



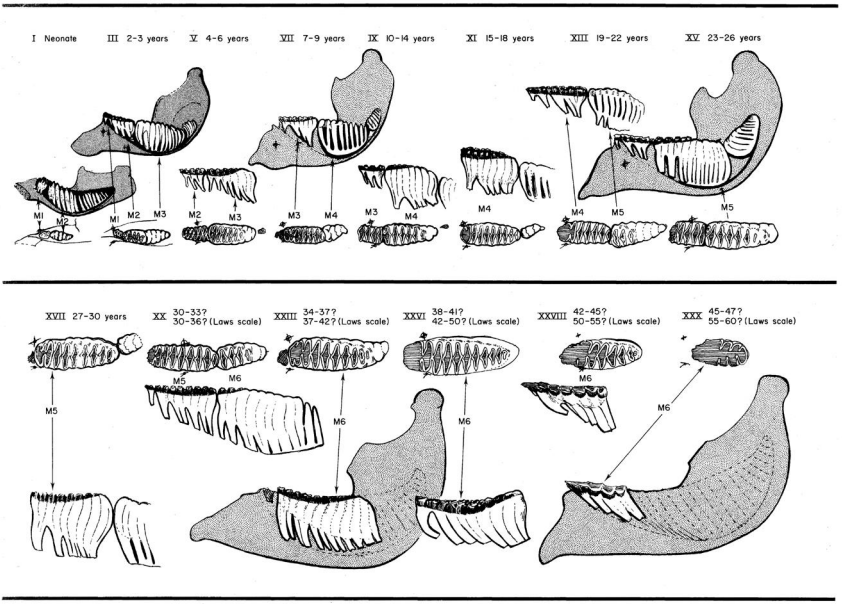
Elevation of proboscid feeding zones through time.

The earliest fossil, *Phiomia*, dates from about 35 mya and appears to have been a swamp-dwelling equivalent of the modern tapir. *Gomphotherium* (25 mya) shows that, as size and weight increased, limbs had to become more like columns. Both tusks and trunk became progressively elongated. By 7 mya *Stegotetrabelodon* had become tall, heavy and long-trunked but retained tusks in both upper and lower jaws. Improvement in the mechanics of chewing led to a rapid decline and elimination of the lower tusks but vestiges of their bony sleeves can still be traced in the lower jaws of living elephants (particularly in the Forest Elephant, *Loxodonta cyclotis*).

The direct ancestors of the African and Asian elephants and the mammoths split into three lines about 5 mya but reached their greatest diversity (at least 10 species) by less than 1 mya. Just as elephants were reaching the peak of their evolutionary and ecological success they became prey to a new predator – humans. Directly or indirectly, as a result of human activity eight species of elephant have become extinct within less than half a million years.

ELEPHANTS ELEPHANTIDAE

Modern elephants evolved in Africa with startling rapidity and seem to owe their later success to an adaptive shift out of very wet, marshy environments into drier, more open and difficult habitats where they became the prime specialist in bulk-feeding on coarse vegetation. To cope with rougher diets their teeth became heavy-duty 'rasp-grinders': single molars set in very short jaws. In the course of a lifetime six cheek-teeth succeed one another, travelling very slowly along the jaw at an angle that wears them away from front to back. Each in turn drops out once its grinding surface is used up. After the sixth tooth the sequence has run its course and the toothless elephant dies. Elephants are thought to live longest where wear of the teeth is slowest and their life-spans may range from about 50 to no longer than 65 years.



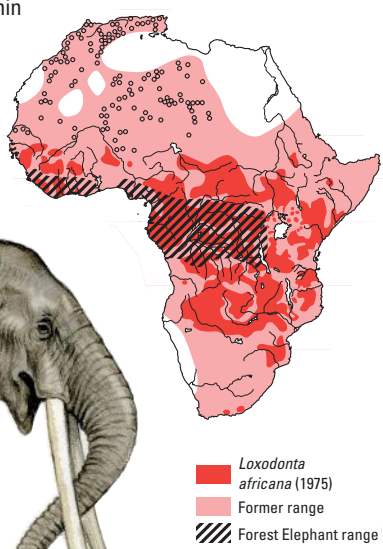
Toothwear and succession in the Bush Elephant. Roman numerals are 'Laws' age scale'. Molariform teeth are numbered 1 to 6. M1 to M3 are equivalent to milk molars in non-proboscids.

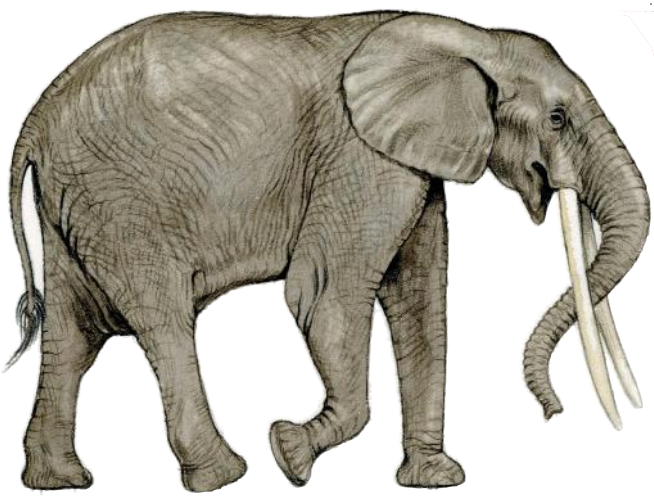
Linked with long life and very large size are slow growth and many years of slow maturation. This in turn demands tightly knit social groups that are both durable and reliable, not least because of the dangers to youngsters from large predators. Adult elephants are invulnerable to all living predators, except humans, but young calves are not. Maintaining complex social bonds with dozens of 'clan' members and many hundreds of regular acquaintances demands memory and intelligence of a high order. Because of a long learning period within a stable (and often very mobile) social group, elephants build up a highly flexible, multifaceted relationship with the environment, its changing resources and the other animals that inhabit it. Learnt skills help them to weather substantial fluctuations in climate and vegetation. Similar advantages were clearly shared by mammoths, *Mammuthus*, in Ice Age Eurasia and North America and by the Indian Elephant, *Elephas indicus*, in S Asia. Throughout some 4 million years of climatic instability *Elephas* was a highly successful species in Africa as well, becoming extinct there as late as about 20,000 years ago. By contrast, today's African elephants, *Loxodonta*, are absent or rare as fossils. The most likely explanation for this is that their ancestors became specialised for life in the moist forests (where bones seldom fossilise). Here the very distinctive Forest Elephant, *Loxodonta cyclotis*, still exists. It is now well known that mammal populations can change their body size over very short periods of time, so the Forest Elephant's emergence has probably been followed by just such a

secondary enlargement. In the first edition of this guide African elephants were treated as a single species. In the intervening years convincing genetic evidence for two species has been published. Nonetheless, Forest and Bush Elephants are very closely related and retain much in common. Much less intensively studied, the Forest Elephant profile must necessarily be briefer and focuses on identifiable differences. African *Loxodonta* species were probably beneficiaries of the *Elephas* extinction. However, the human hunting skills that probably helped to destroy *Elephas* in Africa have now been honed on *Loxodonta* and may well bring about their extinction as well. Only a collective human will to preserve elephants and their habitats can save them now.

FOREST ELEPHANT *Loxodonta cyclotis*

OTHER NAMES Fr. *Eléphant de Foret.* Ger. *Waldelefant.*
MEASUREMENTS Sh.ht 1.6–2.4m (♀), 1.7–2.8m (♂). T 0.5–1.2m. W 900–3,000kg (♀),1,200–3,500kg (♂).
RECOGNITION Tall, long-legged, large-eared, short-necked grey animal with trunk and tusks. Forest Elephants differ from Bush Elephants in overall size, in more rounded ears and more slender tusks (of harder ivory). Feet tend to differ in retention of more nails in Forest Elephants (five nails on forefeet, four on hindfeet).
GEOGRAPHIC VARIATION A tendency for precocious growth of the tusks in young males and their early separation from their maternal groups misled early observers into supposing that such small animals were a distinct 'pygmy' or 'dwarf' species or subspecies. No other evidence for variation has been observed.
DISTRIBUTION Originally throughout western and central African forest zone. Now vestigial populations are being eliminated completely as sophisticated firearms fall into the hands of unsophisticated poachers. African governments within the rainforest zone seldom have the power or the inclination to discipline or disarm the practitioners of highly profitable poaching networks. On current projections Forest Elephant range will continue to shrink and no mapping of its range is likely to be accurate for very long.
FOOD Forest Elephants were originally able to subsist on fruit for much of the wet season. Up to 70 species of fruits have been recorded. Distribution and periodicity of fruiting largely determined elephant movements within the forest during the rains. Foliage and bark are mainly eaten in the dry season. Grasses are only grazed at marginal times and in marginal habitats. Mineralised earths are commonly excavated and may be consumed in substantial quantities.





BEHAVIOUR Forest Elephants seldom aggregate into large groups. Ranging from 2–20 individuals, family groups average out at about three individuals. Groups centre on a female and her offspring, with males leaving the maternal group earlier and more consistently than female offspring. Females mature at 12–14 years and may stay with their mother after parturition or form their own nuclear family. Gestation is about 660 days. Males come into musth for up to two months at a time and mainly during the dry season. Females only exhibit activity of the temporal glands during extreme stress. Lactating females have been observed suckling baby elephants that were not their own offspring.

There is a strong preference for diurnal activity. Individuals are highly 'talkative' with both audible and ultrasound signalling frequent and varied. Forest Elephants maintain conspicuous paths in the forest, a habit that facilitates their killing by poachers.

ADAPTATIONS Recent studies of the genetics of Forest Elephants in central West Africa have corroborated my suggestion (1976) that these could be dwarfed ecological isolates descended from the extinct *Loxodonta adaurora* (last fossils 2 million years old). If so, Forest Elephant populations could represent a particularly ancient lineage at the centre of their distribution. Less conservative populations may traverse the same region (between Cameroon and the Congo R.) and certainly occur in other parts of the *L. cyclotis* range. If Bush Elephants have derived from these small forest animals their enormous size must be a very recent and secondary development. Contrasts in size and habitat could inhibit mixing but there are undoubted periods and areas where 'hybridisation' takes place between Bush Elephants and Forest Elephants. There are also places where they co-exist as separate entities without genetic mixing.

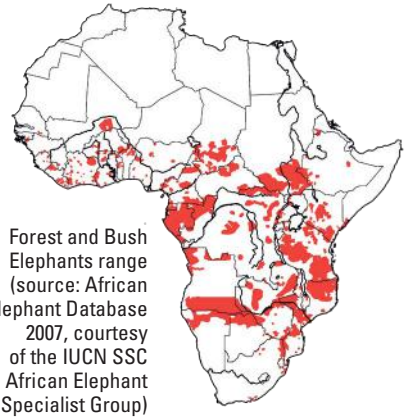
STATUS Although all trade in Forest Elephant ivory is prohibited by international treaties, bushmeat and ivory poaching remains relatively open and without regulation over much of its range. Eliminated from most of its former range, further depletion is now exceptionally rapid through widespread use and trade in automatic firearms. Logging concessions now operate over the greater part of this species' range and logging companies generally collude in the killing and transport of meat and ivory. Elephant family members are reluctant to abandon one another or disperse, and a single armed poacher can therefore dispatch or wound all members of a family group. In this way it is common for up to 10 elephants to be killed at the same time. Illicit bushmeat hunting and steel-wire snaring inflict cruel and ever-more pervasive suffering upon remaining populations.

BUSH ELEPHANT *Loxodonta africana*

OTHER NAMES Savanna Elephant. Fr. *Eléphant d'Afrique*. Ger. *Afrikanischer Elefant*. Swah. *Ndovu*, *Tembo*.

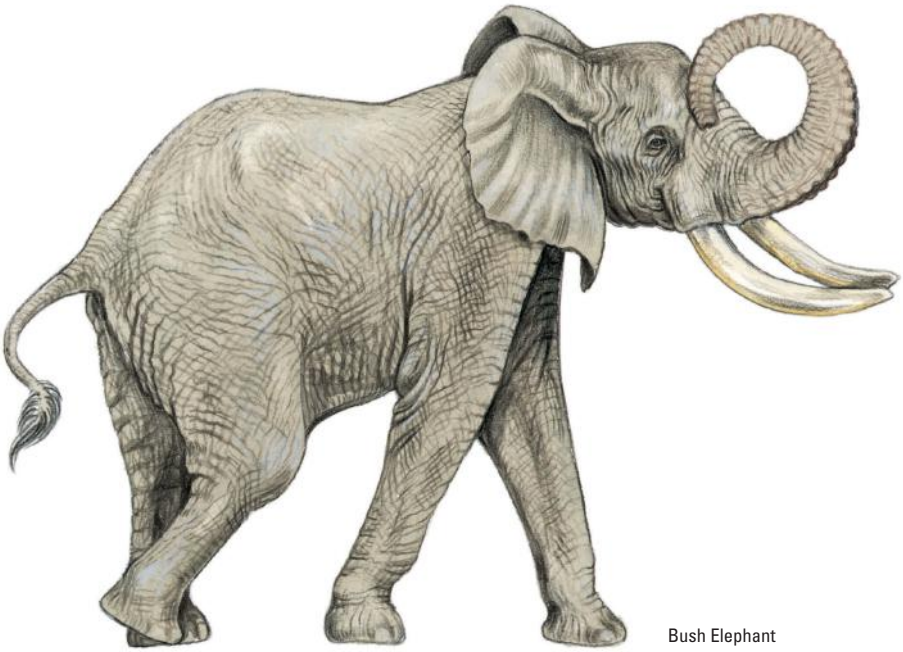
MEASUREMENTS Sh.ht 2.4–3.4m (♀), 3.0–4.0m (♂). T 1.0–1.5m. W 2,200–3,500kg (♀), 4,000–6,300kg (♂).

RECOGNITION The largest land animals, Bush Elephants are easily identifiable in having a trunk, tusks, large ears and pillar-like legs (see also Forest Elephant). Their thick skin is only superficially pigmented and the intensity of the melanin layer varies from a dense black to pale grey, brown or, in rare instances, depigmented pink (in patches or overall). Newborns are often very hairy and adults retain coarse, short bristles on the trunk, chin and, as abraded remnants, in the crevices over much of the rest of the body. The large, round ears are not only sound-catching dishes and flagging devices but also a cooling mechanism. The backs of the ears are laced with blood vessels that help to reduce overall body temperature when the ears are fanned. The tusks are modified incisors composed of layered dentine and their presence or absence, size, shape, orientation and microstructure are subject to much variation.



Forest and Bush Elephants range (source: African Elephant Database 2007, courtesy of the IUCN SSC African Elephant Specialist Group)

The feet are columnar, with the original five toes bound into a hoop of tissue, skin and nail above a cushion of elastic tissue. Nails vary from five on both fore- and hindfeet to four on the forefeet and three on the hindfeet, the latter being the norm in Bush Elephants. The smooth but cracked foot



Bush Elephant

pads leave individually recognisable tracks, circular for the forefeet, smaller and more elongated for the hindfeet. Tracks, frequent boluses, occasional urine puddles and extensive harvesting of plants are the most commonly seen signs of elephants. Elephants of both sexes and all ages have temporal glands behind the eye which secrete a liquid called temporin. The flow of this secretion becomes visible (and presumably smellable) when the elephant is excited, or during periodic male 'musth', as does the plasma flowing from the penis of males in musth.

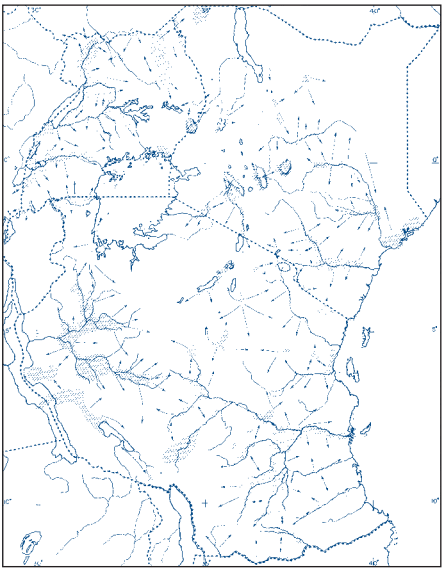
GEOGRAPHIC VARIATION Because successful adaptation to peculiar ecological conditions depends upon long-maintained family traditions, elephants readily evolve subpopulations. These can show consistent characteristics in size, ear shape, limb or pad proportions, skull and tusk shape, number of nails, skin texture and colour. As a result, 25 subspecies have been proposed, but see Adaptations below.

DISTRIBUTION Formerly most of Africa except the driest regions of the Sahara. Even so, their ability to forage as far as 80km from water greatly augmented their overall range in otherwise marginal areas. Conflict with farmers increases as the latter continue to expand into the elephants' remaining pockets of range. However, most attrition is due to the illicit ivory trade for mainly Asian markets.

HABITAT All major vegetation types, usually more than one being included within the annual cycle. The Bush Elephant's dependence on shade and water is well illustrated by the pattern of dry-season retreat into forests and swamps (shown for East Africa). This could be influenced by the short time (about 10,000–20,000 years ago) since they expanded into drier regimes. Although elephants mainly eat the plants that are available they have preferences and dislikes, which results in the local disappearance, selective survival and dispersal of particular plants and plant communities. In this way elephants have been a major influence on most vegetation communities for many millennia. The physical impact of elephants is also evident in browse lines, broad pathways, sunken waterholes, 'ploughed' soil and caves excavated for salt.

FOOD Grass and browse are taken in different and changing proportions by season (see above). Elephants consume about 5% of their body-weight (i.e. up to 300kg) in 24 hours and vegetation takes about 12 hours to pass through the animal. The bush-bashing that is typical of many male ungulates has a nutritional byproduct for the elephants. Trees are most frequently felled by young

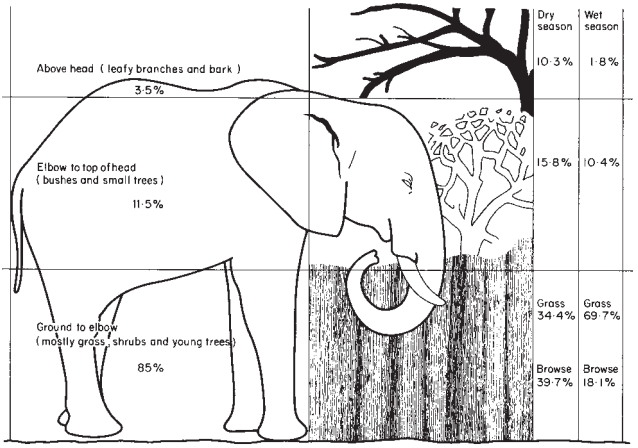
Season	Ecological Conditions	Elephants
DRY	Fires and destruction of grass	Move towards refuge areas Avoid fires and human activities
	Flood plains dry but grass still growing	Move on to flood plains Temporary concentrations in borassus groves
	Surface water finished	Move to hills, forests or rivers for permanent shade Less feeding, more resting Barking trees
Early rain		
WET	Flushes of green growth	Major movement initially by males Concentration on localised pastures, followed by dispersal
	Rapid growth everywhere	Longer feeding, more active
	Some valley soils gluey	Avoid slippery, sticky soils
	Grass long	Well dispersed in grasslands and savanna
End of rain		



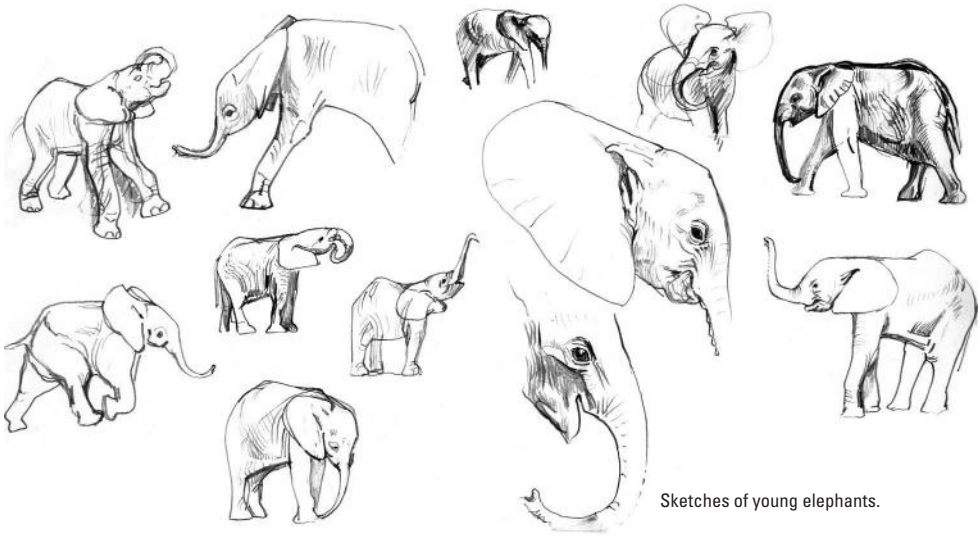
Dry season refuge areas with wet season dispersals suggested by arrows. The map summarises knowledge of seasonal movements. Elephants have now been eliminated in a number of areas shown here. (Data from Brooks and Buss, 1962a; Lamprey, 1963; Cobb, 1976; Uganda, Kenya and Tanzania Game Dept. records; and personal research.)

or solitary males, so obtaining out-of-reach fruits, leaves, pith or branches may not be the only reason for such behaviour. The crash of a felled tree sometimes attracts families or other solitary males and the arrival of the latter may precipitate chases and contests.

BEHAVIOUR The central social unit is the mother and her offspring. Female elephants are not able to conceive until 8 years of age (20 at latest), but once they become mothers they soon become unit leaders, or 'matriarchs'. Bush Elephants find it easier to forage, find one another and travel in larger groups but even here the nuclear family tends to split by the time there are 10 daughters and grandparents. Nonetheless, closely related 'matriarchal' groups in the same vicinity maintain frequent and friendly meetings for many years. These and larger associations have been variously labelled 'bond-groups' or 'clans'. Males are driven out of these associations at about 10–14 years of age. They may join with other males but tend to choose partners that are either substantially



Elephant feeding levels.



Sketches of young elephants.

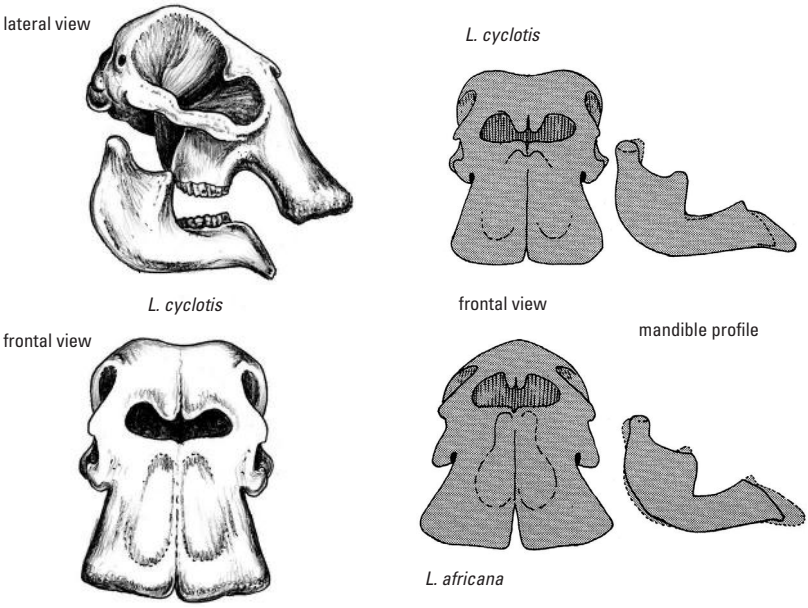
younger or older than themselves in an informal, linear hierarchy. Dominance is less a feature of female groups but age, size and health determine the 'matriarch' in large family groups. Very aged or permanently disabled females are forced to drop out of their groups.

Female elephants are frequent 'talkers', using rumbles, growls, roars, snorts, squeals and trumpets to convey a variety of signals, conditions and emotions. The most remarkable part of their repertoire, infrasound, was first described by scientists only in 1987.

Females come into oestrus for 2–6 days after an interval of anything between 3 and 9 years. Their advertisement of this rare and vital condition depends on a unique sequence of sounds emitted at below the threshold of human hearing but perceptible at least 4km away and, depending on the weather and topography, sometimes much further. Females routinely use infrasound to keep in touch with and monitor other groups in their clan or regional population. Males are more silent but passively eavesdrop until the unmistakable mating song is heard, whereupon all males within range immediately hasten towards the singer, the fastest and most urgent suitors being those that are in 'musth', periodic rutting behaviour marked by a continuous flow of temporin lasting 1–103 days. Rutting males also develop a swollen, semi-erect penis that dribbles urine and a greenish fluid. Tests have shown that the aggressiveness of musth bulls is linked with high levels of testosterone. Males in this condition appear to intimidate all other classes of elephant but are the preferred partners for oestrous females, who benefit from their close (but not continuous) attention because they discourage the attentions of numerous other males.

Gestation lasts 650–660 days and one, very rarely two, young are born, with a slight peak of births in the rains. Although they rise to their feet within hours, newborns are visibly unsteady for several weeks (a feebleness that attracts Lions and hyaenas). Mothers are alert to all their infant's needs, helping it over all manner of obstacles with trunk and feet. They are particularly sensitive to any signs of dehydration and, in the absence of other sources, will regurgitate water from their own stomachs. Mothers will pump water directly into their infants' mouth and will squirt and massage it while playing in shallow water. Although calves can survive on solid food before they are 2 years old, mothers tend to remain in milk for about 4 years (some lactate continuously throughout their reproductive life). Offspring become independent at varying rates; some scarcely leave their mother's side until they are nearly 10 years old (an age at which some will already have calves of their own). Body size and the development of tusks are also very variable, making overall estimates of age by height or tusk length difficult. In the case of dead elephants, jaws provide a reliable measure of age (see p.57).

ADAPTATIONS Before widespread and recent extinctions, species of elephants were diverse, abundant, highly successful and actively evolving new forms in special habitats and on many

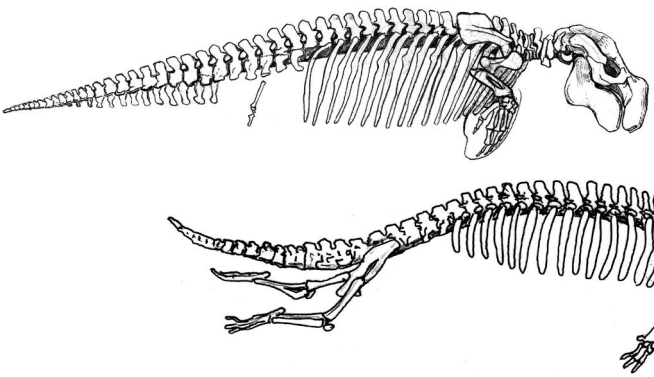


offshore islands. On a much smaller and shorter scale, modern African elephants had begun to diverge along similar lines: e.g. desert specialists in Namibia, dwarfs in the Atlas Mts. In the swamps of the R. Rufiji delta a trend towards particularly large ears, a smooth skin and tuskless jaws shows that families and subpopulations can maintain peculiar, possibly adaptive, traits even in the absence of complete isolation. Numerous features of the Bush Elephant's biology, especially its sensitivity to dehydration and heat, suggest that adaptation to arid environments is a recent and ongoing process. The surviving populations of elephants, small and scattered as they are, still exemplify great diversity and continuous adaptation to climate and the new challenges posed by human control of their environment.

STATUS Recent surges in elephant killing across Africa have provoked calls for international conservation action. Declines, fluctuations and elimination of elephants in Africa is not new. They were first eliminated from North Africa by about the 4th century AD through a combination of ivory-hunting and increasing aridity. Then they were exterminated by the settlement of South Africa during the 18th and 19th centuries and over much of West Africa in the 20th century. Low ivory prices and legal protection between 1920 and 1970 allowed an extensive recovery in much of tropical Africa, only to be followed by massive declines in the 1980s as new business interests, as well as corrupt politicians and soldiers, organised the wholesale killing of elephants for ivory. From between 5 million and 10 million in the 1930s and 1940s, African elephants have declined to between half a million and three-quarters of a million at the present time. Numerous bodies exist to protect elephants, both nationally and internationally. The ultimate success of all these initiatives depends upon long-term, sound education and sustained, honest management at the most local level.

SEA-COWS SIRENIA

The name Sirenia derives from the legendary 'sirens', so-called 'mermaids'. Fossil forms are known to have grown up to 10m in length. They share terrestrial origins with elephants and, unlike most other aquatic mammals, they subsist almost entirely upon flowering plants growing in rivers, estuaries and the sea. The evolution of sea-cows seems to be associated with the Tethys Sea (precursor to the Mediterranean). There are two extant families of sirenians: Dugongidae, along Indo-Pacific shores, and Trichechidae, in waters surrounding the tropical Atlantic.



Fossil skeleton of an extinct quadrupedal sirenian, *Pezosiren* (*below*) compared with the skeleton of the extant Dugong *Dugong dugon*.

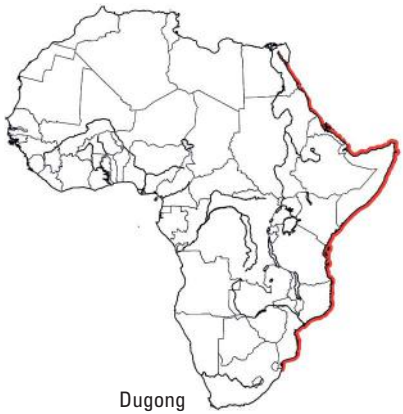
DUGONG DUGONGIDAE

This family has just a single representative.

DUGONG *Dugong dugon*

OTHER NAMES Fr. *Le Dugong*. Ger. *Dugong*. Swah. *Nguva*.
MEASUREMENTS HB 2.4m (2.2–3.31m) (♂). Flippers 300–420mm. W 250–420kg.
RECOGNITION The entirely aquatic Dugong is a large, grey torpedo-shaped animal with horizontal, whale-like tail-flukes. Externally there is no suggestion of neck or upper arm, both being contained within the regular, cylindrical form of the body. The forearm and hand form simple paddles which have a stabilising function and are occasionally used to free food plants in sand. The main propulsive force is provided by undulating movements of the tail-flukes and body. Small lidless eyes

adult male



Dugong

are embedded in blubber. Ears appear as minuscule openings on either side of the head. Anus and genitalia surface in a single, elongated aperture in females but the penis extrudes in males from an aperture midway down the lower belly. Testes are abdominal.

While lactating, the mammary glands resemble human breasts, hence the mermaid myth. Six cheek-teeth erupt during a Dugong's life, but never simultaneously. The peg-like molars are shed until only two remain. The second upper incisor develops a tusk-like form within the sharply down-turned maxilla in mature males (and the occasional old female). Dugong tusks build up layers that can be used to age individuals.

The rudiments of tooth cavities grow ligaments that anchor robust horny plates to the anterior jaws. On the rostrum of the premaxilla there is a tough, gristly knob around which modified bristles in the lips close while the animal is feeding. Bristles in the upper lip act like mobile rakes and interlace with thick, short bristles in the lower lips as they close over the growing sea-grasses that comprise the bulk of the Dugong's food. This raking action is operated by huge lip muscles on either side of the down-turned muzzle. Valvular nostrils lie just behind this lip-mass and are often all that can be seen of a surfacing Dugong from a passing boat.

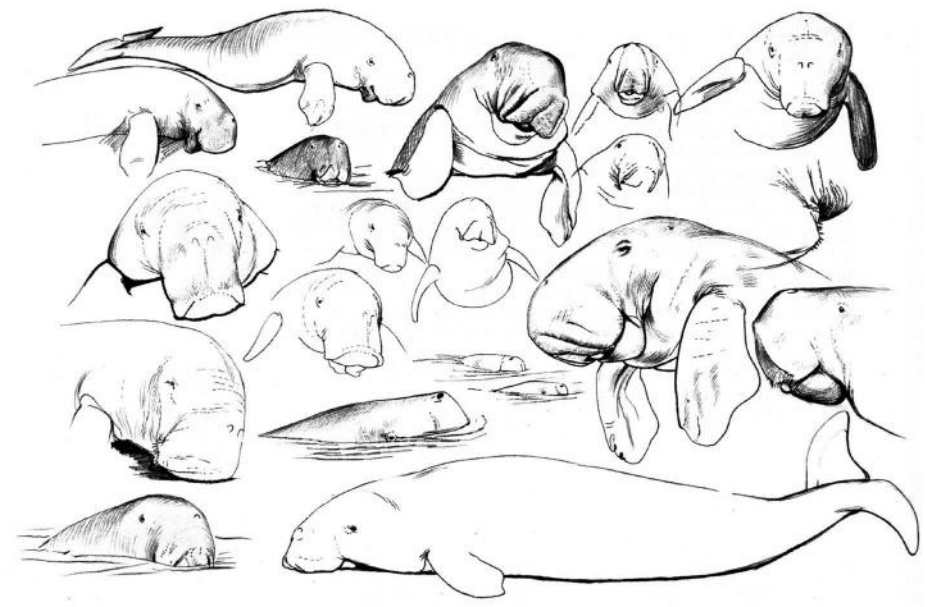
GEOGRAPHICAL VARIATION No subspecific or regional differences have been recorded.

DISTRIBUTION Formerly found in all tropical and subtropical waters of the Indian and western Pacific Oceans. Original range correlated with the marine angiosperms on which Dugongs feed. African range from Red Sea and Gulf of Aden to Mozambique with vagrants as far south as KwaZulu-Natal.

HABITAT In Africa, in coastal waters with a preference for protected bays and the lee of islands with extensive, albeit seasonal, beds of sea-grass. Around the Lamu archipelago, fishermen reported that Dugongs used to be numerous in deeper waters beyond the reef during the NE monsoon (November to March) when the sea was calm. When the sea became cooler and very rough during the SE monsoon (April to October) Dugongs moved into shallower, more sheltered bays within the reef. Similar seasonal movements have been reported by fishermen around Mafia Is..

FOOD Sea-grass grazers and 'rootlers', Dugongs yank up entire plants, leaving bare patches of rootled mud or sand in sea-grass swards. Their coarse graze/rootle feeding probably helps maintain 'rapid-repair' sea-grasses such as *Halophila* and *Halodule,* species that are both nutritious and easily digested. As noted above, seasonal movements between off-shore and in-shore pastures off the Kenya coast have been reported. Such movements are attributable to seasonal change in marine angiosperms, to fluctuations in water temperature and to roughness of the sea. According to experienced fishermen, deep-water sea-grasses, notably *Cymodocea and Syringodium*, were grazed by Dugongs between November and March, when seas are calm and warm. Shallow-water, in-shore species such as *Halodule, Halophila* and *Zostera* were reported being grazed between April and October, when off-shore waters were rough and cold and apparently avoided by Dugongs. Crabs have been found in Dugong stomachs and fishermen report Dugongs eating molluscs, but it is possible that such foods are incidental 'by-catch'. Dugongs have a herbivore's elongated hindgut, appropriate digestive microflora and long retention times. They have been reported to consume some 25–30kg of sea-grasses daily.

BEHAVIOUR The only known long-term association comprises a cow and her calf, and most sightings are of one or two animals. Fishermen report small groups surfacing simultaneously and briefly peering around. Estimates of about 100 animals were still to be seen off Pate Is. in the early 1960s. In tropical Australian waters as many as 44 individuals have been recorded travelling up to 560km. Groups of male Dugongs have been reported to fight energetically in competition for females. Females seemed to gravitate towards large individuals (presumably males) that seemed to defend small patches, possibly clustered in breeding grounds or 'leks'. Chirps and ultrasonic sounds have been recorded. Dugongs make a whistle that fishermen claim elicits a defensive buffeting action from presumed males. Dugongs spend most of their time in shallows less than 3m deep. On average they dive for 2.6 minutes, and dive about 11 times per hour. The maximum recorded dive depth was 20.5m, with maximum time below the surface 12.3 minutes. Dugongs in Australia can live as long as 73 years; females are 6–17 years old when they bear their first calf. Gestation of a single calf (only very rarely twins) is approximately 13 months. Offspring are suckled for about 18 months. Birth intervals are very variable (estimates from 2.5 to 7.0 years). Young grow rapidly and start grazing soon after birth. Slow turnover rates corroborate estimates that suggest any population is unlikely to be able to increase in size more than 5% per year, and then only while enjoying near zero predation.



Sketches of Dugong. Note the crescent-shaped valvular nostrils, and how the ventral surface follows the same plane as the grazing mouth.

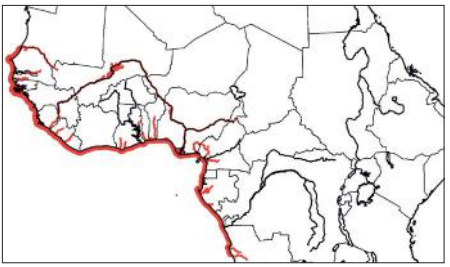
ADAPTATIONS The most obvious adaptations all concern an aquatic existence. This is evident in their large size, streamlining, whale-like tail, flippers and effective loss of hind limbs. Dense, heavy bones, especially the marrow-less ribs, help counteract the buoyancy of large lungs while animals are feeding on the sea floor. Bristles around the lips provide an effective 'rake', bringing food into the mouth. The nostrils open immediately behind the point where the muzzle angles downwards; this permits breathing with minimal exposure above the water. Lidless eyes are lubricated by oil glands and protected by nictitating membranes. The cerebrum of the brain is small and somewhat foetal-like in structure. By contrast the cerebellum (associated with balance and orientation) is well developed.
STATUS While fishermen name themselves and sharks as predators of Dugongs, the very slow reproductive rate of Dugongs suggests that before humans invaded marine ecosystems sirenians somehow managed to keep predation to a minimum. In Africa today, as elsewhere, Dugong numbers continue to decline catastrophically. In addition to deliberate and accidental netting and spearing, oil spills and damage to sea-grass beds by trawlers are thought to affect Dugongs. A huge expansion of human populations around the Indian Ocean littoral and concomitant intensification of netting has hit Dugong populations hard. Although they are protected by law in most eastern African countries, authorities are unable to monitor or protect them. Unless active, Dugong-specific conservation policies are put in place, these animals will become extinct over most of their African range.

MANATEES TRICHECHIDAE

This family embraces three species of manatees, the African representative, the West African Manatee *Trichechus senegalensis*, the Amazonian Manatee *T. inunguis* and the West Indian Manatee *T. manatus*. The somewhat ovoid but streamlined body ends in a single, large, flat and rounded tail-fluke. Blunt, paddle-like flippers protrude from a rotund, bloated body. Manatees usually swim slowly, dive to shallow depths and for short periods of time (<20 minutes). They have a low metabolic rate and much enlarged hindgut. Although wholly aquatic, they can raise themselves sufficiently out of the water to browse. The most important channel for communication among manatees is auditory. Vision is weak, especially in turbid waters. Apparent responses to chemical and electrical signals await investigation. Florida Manatees can live 60 years.

WEST AFRICAN MANATEE

Trichechus senegalensis



West African Manatee

OTHER NAMES Fr. *Lamantin*. Ger. *Seekuh, Manati*.

MEASUREMENTS HB 2.56m (1.77–3.34m) (♂), 2.59m (2.25–3.03m) (♀). W (est.) 166–640kg.

RECOGNITION Effectively wholly aquatic, with rotund body, blunt flippers and a single, very large and rounded tail, a broad back and small head. Like Dugongs, they have sphincter-ed lidless eyes and no external ears. The small, relatively short rostrum of the muzzle bends slightly downwards. In common with some other aquatic animals with bare skin the body colour tends to be determined by local epiphytic algae, varying from green-ish, brown or black to grey: in coastal waters barnacles may find a pur-chase. Their textured skin is covered by sparse, very fine and evenly dis-tributed hairs. A thick layer of blubber and fat effaces all underlying ana-tomical features, making them look like gigantic maggots. Three or four of the flipper digits have keratinous fingernails along their margins. Females have two axillary mam-mae and a genital slit adjacent to the anus. The male penis is generally concealed within an aperture in the middle of the lower belly. The maxilla and premaxilla of the carunculated skull are less downwardly deflected than in the Dugong.

GEOGRAPHIC VARIATION None known.

DISTRIBUTION Until recently West African Manatees occurred along most of the coastal regions, rivers, estuaries and lagoons of West Africa from southern Mauritania to central Angola. They occur deep in the interior, living along the courses of most major rivers as well as offshore in coastal shallows wherever there are abundant sea-grasses. They have been reported from L. Chad but confirmed records are lacking.

HABITAT Mainly riverine, West African Manatees also inhabit coastal lagoons, estuaries and bays where sea-grasses and other aquatic vegetation can grow. Some populations have become wholly isolated inland by natural changes in river courses such as oxbow lakes or behind cataracts that are now impassable. Likewise, hydroelectric and other dams have served to isolate inland populations. On the outer margins of their ecological tolerance, where water levels drop drastically during dry seasons, these manatees have been found to survive in deep pools and temporary lakes. Alternatively they may escape drying out by making seasonal or periodically forced movements downriver.

FOOD Manatees consume a wider range of plants and their parts than Dugongs. This is mainly because their mouthparts are more versatile. While both species prefer sea-grasses, manatees can also handle and browse items such as floating vegetation and plants that overhang banks and eyots. Floating fruits and nuts are also readily snatched from below. Recorded preferences include both submerged and exposed leaves of mangroves, aquatic floaters such as *Eichornia* and *Cymodocea*, and some widespread marsh-grasses such as *Vossia* and *Echinochloa*. Manatees enfold a plant with their lips and tug or twist until the item tears away. Such broken vegetation in amongst untouched bank plants signals recent manatee browsing. During flood seasons manatees may damage rice paddies. Since a free-ranging adult has been estimated to consume as much as 8,000kg of vegetation in one year, impact on a farmer's crop can be significant.

Radio tracking has shown that manatees mostly feed at night and that they spend 4–6 hours feeding, sometimes travelling several kilometres between daytime resting areas and pastures, to which they may return for several nights. It is likely that such travel and night feeding are behaviours induced by human disturbance.

BEHAVIOUR In general, both sexes are predominantly solitary, but females maintain a close link to their current offspring. Females in oestrus often attract a following of males and aggregations may form at choice pastures or safe refuge sites. Radio tags have shown that seasonal aggregations formed just before the rainy season along a short length of a minor river in Côte d'Ivoire. This observation suggests seasonal breeding, possibly focused on traditionally favoured waters. Changes in the temperature, saltiness and levels of their waters are also known to induce local movements. Thus animals shift upstream or downstream in response to a variety of cues. Gestation is 12–13 months. Both births and mating peaks have been reported just before the onset of the wet season but newborns have also been reported throughout the year.

ADAPTATIONS The shape of a manatee, like that of a whale or fish, is adapted to an aquatic life but its rotund bulk is less suited to sustained speed. Even so, a very wide, rounded tail-fluke is capable of propelling the animal's massive body into a relatively fast, mud-churning spurt. Thus their only defences are escape in turbid water or a glancing buffet from the body serving as a bumper (it is likely that large crocodiles were once a significant risk for manatees). The forelimbs are paddles that help orient the body, hold food and lever the body along in a sort of clumsy trudge across the substrate. They can also be held close to the body to reduce turbulence. The lips and their functional musculature are hugely developed, with rows of stiff bristles embedded in the exceptionally mobile lips, facilitating a firm purchase on vegetation. In the West Indian species, it has been found that fine body hairs, similar to those on *T. senegalensis*, can register changes in pressure and pick up vibrations. Rear teeth migrate forwards as anterior teeth wear out from continuous abrasion induced by their intake of coarse, sandy or muddy grasses. The number of teeth present at any one time therefore varies. As with Dugongs, lungs and diaphragm, in coordination with heavy ballast-like bones, help control buoyancy.

STATUS Manatees survive through much of their historic range but numbers are low throughout. Slow reproduction rates and sustained mortality inhibit any recovery. IUCN classes the West African Manatee as vulnerable; CITES Appendix II. They are widely protected by law but enforcement is minimal. Manatees are hunted throughout their range for meat, oil and body parts (for supposed medicinal effects). They are harpooned, netted and mouth-hooked on large hooks baited with cassava. Many also become incidentally entangled in fish and shark nets or on hook lines.

AFROINSECTIPHILLIA

Afroinsectiphillia, meaning 'African insect-lovers', was first proposed as an important taxonomic grouping (at the level of cohort) in 2001. This clade embraces all non-paenungulate Afrotheria. These are the otter-shrews and golden-moles (Afrosoricida), sengis (Macroscelididae) and the Aardvark (Tubulidentata).

AFROSORICIDS AFROSORICIDA

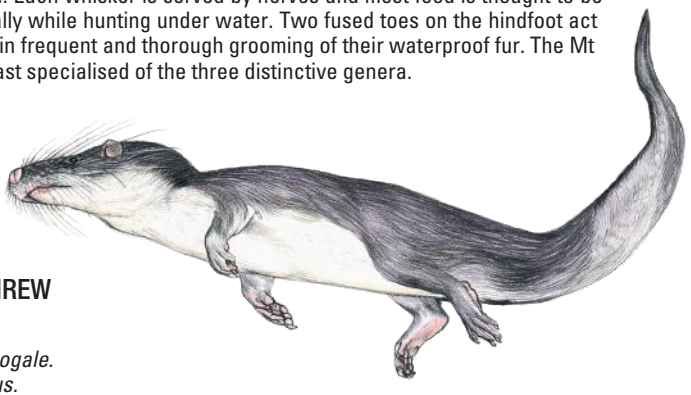
Otter-shrews	Tenrecidae, Potamogalinae
Golden-moles	Chrysochloridae

The order Afrosoricida was erected together with Afrotheria in 1998 because new molecular techniques had revealed that several groups of African and Malagasy small mammals had a distant but unequivocal genetic relationship with hyraxes, elephants, sea-cows and sengis. Although the name was new, Afrosoricida embraced three known mammal families that previously occupied a 'scrap basket' order called 'Insectivora'. These mammals were the Malagasy tenrecs, Tenrecidae, otter-shrews, Potamogalinae, and golden-moles, Chrysochloridae. Other members of the obsolete 'scrap basket' – hedgehogs and shrews – now have their own orders, Erinaceomorpha and Soricomorpha.

OTTER-SHREWS TENRECIDAE, POTAMOGALINAE

Giant Otter-shrew	*Potamogale velox*
Mount Nimba Otter-shrew	*Micropotamogale lamottei*
Rwenzori Otter-shrew	*Mesopotamogale ruwenzorii*

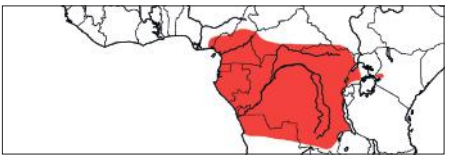
Otter-shrews are the only African survivors of a group that the fossil record indicates was once widespread. Their other contemporary representatives, the tenrecs, are restricted to Madagascar. The three genera are all aquatic and of very restricted distribution. They are distinctive in lacking collar bones or clavicles. They have a flattened muzzle in which very numerous and stiff vibrissae are embedded. Each whisker is served by nerves and most food is thought to be found by touch, especially while hunting under water. Two fused toes on the hindfoot act as combs and are used in frequent and thorough grooming of their waterproof fur. The Mt Nimba species is the least specialised of the three distinctive genera.



GIANT OTTER-SHREW

Potamogale velox

OTHER NAMES Fr. *Potamogale*.
Ger. *Grossotterspitzmaus*.
MEASUREMENTS HB 290–350mm. T 45–90mm. W (est.) 300–950g.
RECOGNITION Aquatic mammal with a brown back and white underside. The broad, flat snout is covered in bristles. Flat shields cover the nostrils. The fur is generally very dense and soft but is short and silky on the bladed tail. Vertical flattening of the tail allows a fish-like, side-to-side swimming motion.
HABITAT Rivers within the main forest block from Nigeria to W Kenya. The Giant Otter-shrew sometimes occurs in large, fast-flowing rivers, as well as streams, sluggish coastal rivers and swamps. It retreats to burrows and crevices on river banks to rest and breed.
FOOD Freshwater crabs, fish, insects, water molluscs and occasional frogs, caught in water at night.
STATUS Widespread but sporadic distribution. Sometimes drowned in nets or fish traps.

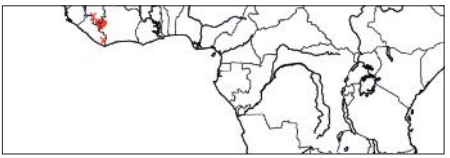


Giant Otter-shrew

MOUNT NIMBA OTTER-SHREW

Micropotamogale lamottei

OTHER NAMES Pygmy Otter-shrew.
Fr. *Micropotamogale de Lamotte*.
Ger. *Kleinotterspitzmaus*.
MEASUREMENTS HB 120–150mm. T 100–200mm. W (est.) 60–90g.
RECOGNITION A small, soft-furred, aquatic mammal, uniformly grey-brown in colour, with a slender, rat-like tail. The feet lack any trace of webbing.
HABITAT Waters in the vicinity of Mt Nimba; montane streams, small rivers, swamps and ditches in surrounding forests, forest–savanna–cultivation mosaics.



Mount Nimba Otter-shrew

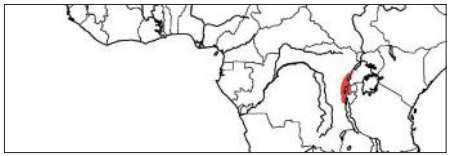
Mount Nimba Otter-shrew

Rwenzori Otter-shrew

FOOD Crabs, fish and insects, mostly hunted at night in the water.
STATUS Mining in Liberia and Guinea destroy habitat and pollute waters. Endangered (IUCN).

RWENZORI OTTER-SHREW

Mesopotamogale ruwenzorii



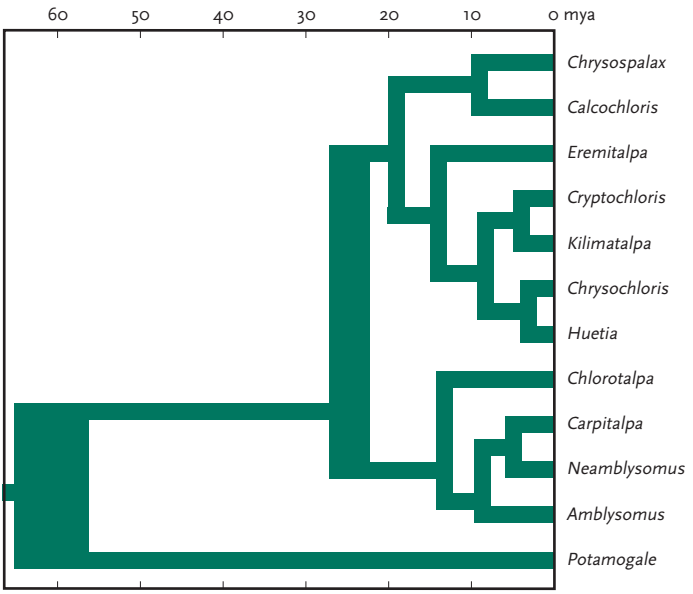
Rwenzori Otter-shrew

OTHER NAMES Fr. *Potamogale du Ruwenzori*. Ger. *Mittelotterspitzmaus*.
MEASUREMENTS HB 123–200mm. T 100–150mm. W (est.) 130–150g.
RECOGNITION Soft-furred, aquatic mammal with a broad, whiskered nose and minuscule eyes and ears. Dark brown above and white below. Hands and feet are partially webbed. The tail, where it is nearest to the body, has a vertically oval profile.
HABITAT Waters flowing off the Rwenzori and Kivu massifs; also likely to occur in Itombwe and has been recorded from montane and lowland streams flowing through forest, savanna and cultivation. Digs burrows in river banks.
FOOD Worms, insect larvae, small crabs, fish, frogs and tadpoles caught at night in water.
STATUS Locally endangered by gold-panning in streams. Near threatened (IUCN).

GOLDEN-MOLES CHRYSOCHLORIDAE

Giant golden-moles	*Chrysospalax* (2 species)
Yellow golden-moles	*Calcochloris* (2 species)
Desert (Grant's) Golden-mole	*Eremitalpa granti*
Cryptic golden-moles	*Cryptochloris* (2 species)
Stuhlmann's Golden-mole	*Kilimatalpa stuhlmanni*
Cape golden-moles	*Chrysochloris* (1–2 species)
Congo Golden-mole	*Huetia leucorhinus*
Forty-toothed golden-moles	*Chlorotalpa* (2 species)
Arend's Golden-mole	*Carpitalpa arendsi*
Lesser narrow-headed golden-moles	*Neamblysomus* (2 species)
Narrow-headed golden-moles	*Amblysomus* (4 species)

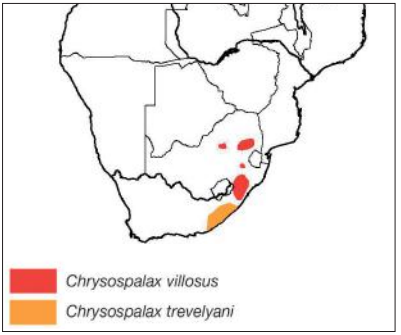
A very ancient and little-known group of subterranean mammals with shiny coats of very dense fur and, externally, a somewhat formless appearance. All have a blunt, bare nose, digging forelegs, with one or more greatly enlarged claws, and less developed hindlegs. They have no visible eyes, ears or tail. Dental differences are so subtle they need a microscope to discern, but skulls provide reliable clues for identification. In palatal aspect muzzles and zygoma form variably angled wedges enclosing genus-specific palates; angles of cranial wedges broadly correlate with soil tractability in their micro-habitats – the harder the soil the narrower the wedge. Likewise, the mechanics of using skulls as wedges renders occipital articulations on the atlas vertebra diagnostic. In lateral aspect the profiles of muzzles and arcs of zygomas are equally diagnostic as are the position and outlines of bullae. They live in various habitats and most obtain the greater part of their invertebrate diet underground. They make various types of molehills and subsurface tunnels that betray their presence. They should not be confused with root-rats and blesmols, which are rodents.



Phylogenetic tree of the golden-moles (mainly after Asher *et al.* 2010).

GIANT GOLDEN-MOLES *Chrysospalax*

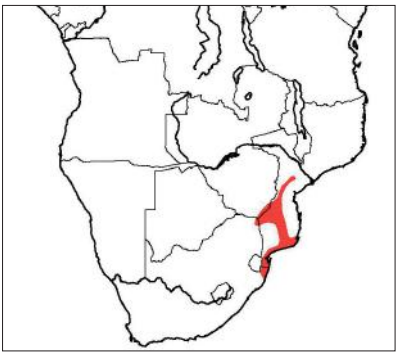
MEASUREMENTS HB 148–230mm. W 125–538g.
RECOGNITION Large golden-moles with a 'double-hull' structure over the braincase caused by an extensive expansion of the cheekbones into rounded bony plates (overlying the temporal muscles). Cranial wedge = 47 degrees. Claws: 3 = long and broad, 2 = long and narrow, 1 = near-vestigial.
SPECIES *C. trevelyani*, *C. villosus*.
HABITAT Deep-soiled areas in forests of the E Cape (*C. trevelyani*) and borders of marshes in drier areas of SE Africa (*C. villosus*).
FOOD Earthworms and other invertebrates.
STATUS Rare and vulnerable.



Giant Golden-moles

YELLOW GOLDEN-MOLES *Calcochloris*

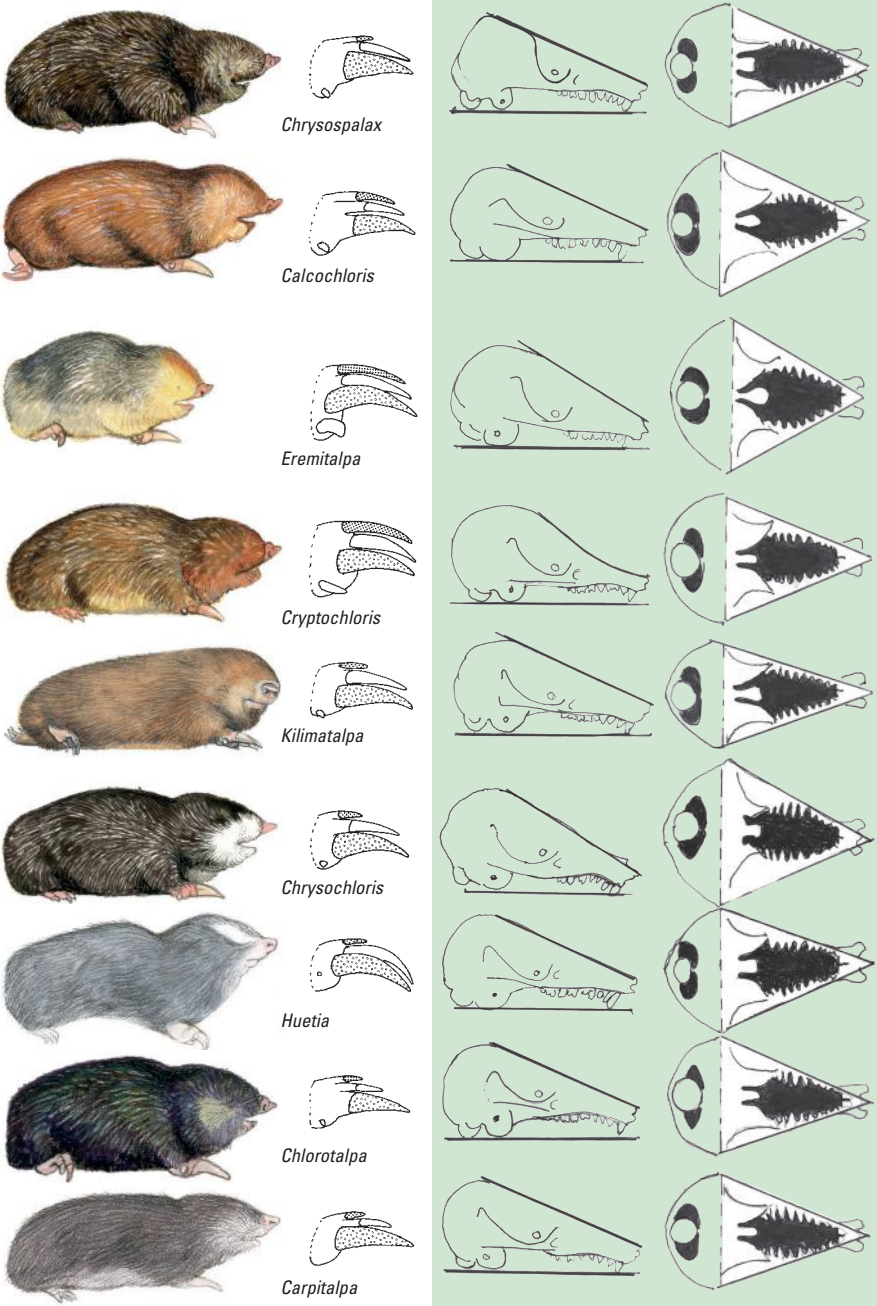
MEASUREMENTS HB 97–108mm. W 20–30g.
RECOGNITION Small, long-bodied species with variably coloured upper surfaces but yellowish underfur. They have 36 teeth. Cranial wedge = 53 degrees. Claws: 3 = medium, 2 = slender, 1 = slender, rel. long.
SPECIES *C. obtusirostris* (*C. tytonis* = uncertain affinity, Somalia).
HABITAT For *C. obtusirostris*, light sandy soils and dunes in S Mozambique and vicinity. For *C. tytonis*, unknown but likely similar in Somali littoral.
FOOD Invertebrates.
STATUS *C. obtusirostris* widely distributed in suitable soils but rare. *C. tytonis* known from one specimen.

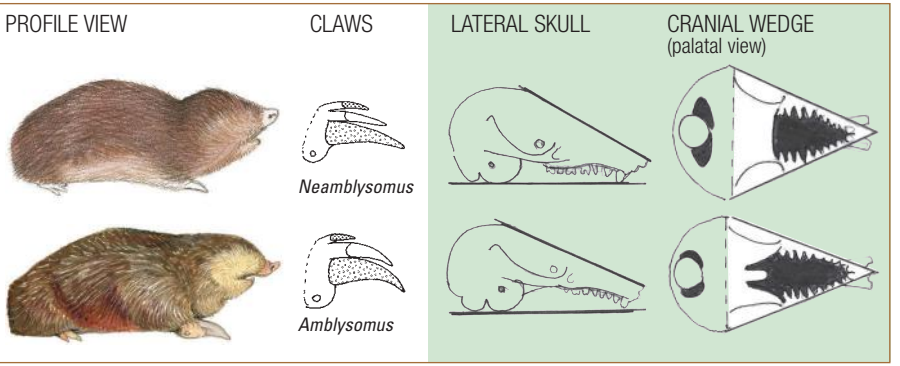


Calcochloris obtusirostris

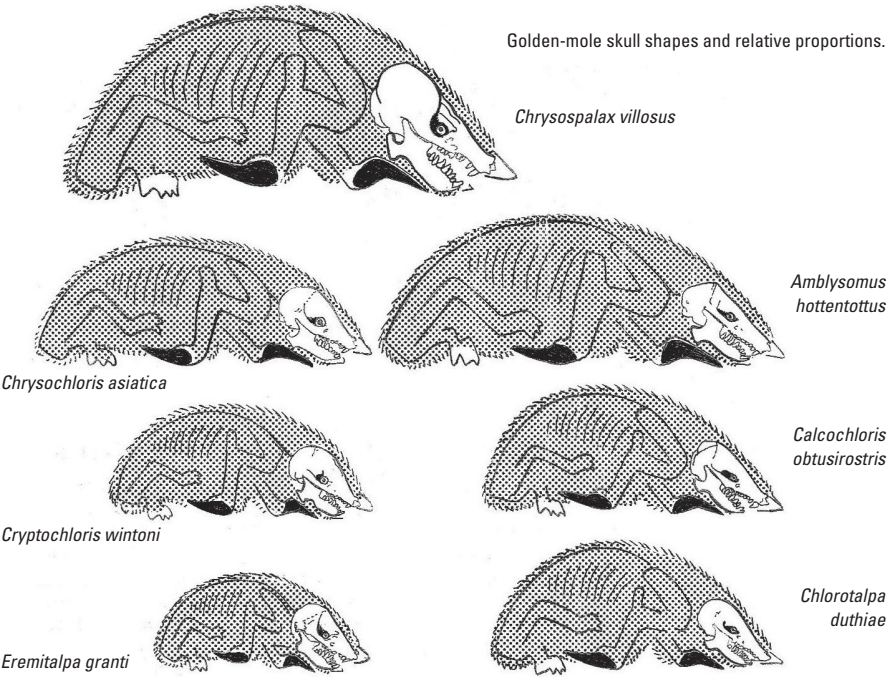
Key to golden-moles (not to scale)

PROFILE VIEW | CLAWS | LATERAL SKULL | CRANIAL WEDGE (palatal view)



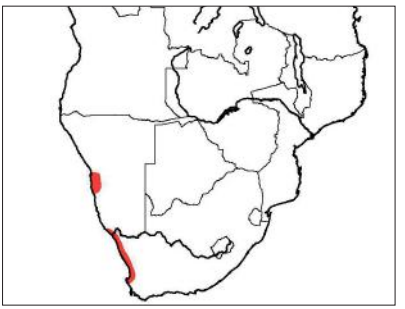


Golden-mole skull shapes and relative proportions.



DESERT GOLDEN-MOLE *Eremitalpa granti*

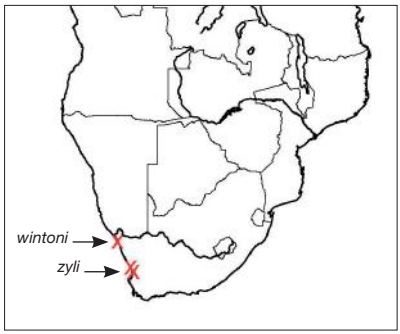
MEASUREMENTS HB 76–86mm. W 16–30g.
RECOGNITION Very small golden-mole with pale silvery fur and a disproportionately large head for a short, dumpy body. It has a short, rounded skull. Cranial wedge = 60 degrees. Claws: 3, 2 and 1 thin and of approximately equal length.
HABITAT Sand dunes along the Namib and Namaqua coastline, preferring areas of dune-grass.
FOOD Insects, spiders and small reptiles, often dug out of dune-grass roots.
STATUS Coastal sands extensively mined for diamonds, but total north–south range extensive.



Desert Golden-mole

CRYPTIC GOLDEN-MOLES *Cryptochloris*

MEASUREMENTS HB 79–90mm. W (est.) 20–30g.
RECOGNITION Small golden-moles with a rounded forehead and skull. The fur has a silvery sheen with grey, white and fawn banding of hairs. Sides are yellowish or brown. Cranial wedge = 45 degrees. Claws: 3, 2 and 1 of nearly equal length (with large pads on the inner sides of the palms).
SPECIES *C. wintoni, C. zyli.*
HABITAT Sand dunes at Port Nolloth and Companies Drift, W Cape.
FOOD Invertebrates, possibly small, sand-dwelling vertebrates.
STATUS Very localised and rare.

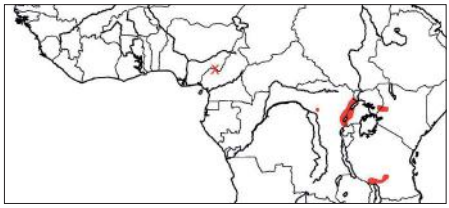


Cryptic golden-moles

STUHLMANN'S GOLDEN-MOLE

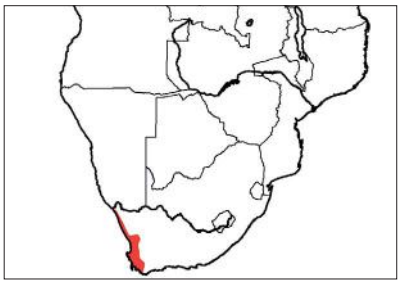
Kilimatalpa stuhlmanni

MEASUREMENTS HB 98–110mm. W (est.) 25–35g.
RECOGNITION Small, metallic-coloured animal with an expanded, rounded back to the skull. Cranial wedge = 38 degrees. Claws: 3 = longest, 2 = shorter and slighter, 1 = very short.
HABITAT East and Central African montane highlands, 800–3,500m.
FOOD Invertebrates, mostly captured underground.
STATUS Locally common and in numerous widespread mountain ranges. Formerly in genus *Chrysochloris*.


Stuhlmann's Golden-mole

CAPE GOLDEN-MOLES *Chrysochloris*

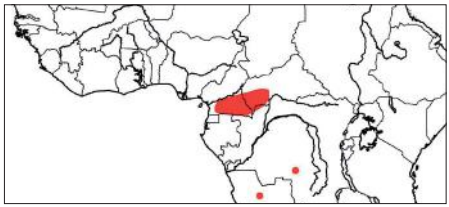
MEASUREMENTS HB 98–110mm. W (est.) 25–35g.
RECOGNITION Small, metallic-coloured animals with an expanded, rounded back to the skull. Cranial wedge = 50 degrees. Claws: 3 = longest, 2 = shorter and slighter, 1 = short.
SPECIES *C. asiatica* (? *C. visagei*, species status uncertain).
HABITAT Cape Province.
FOOD Invertebrates, mostly captured underground.
STATUS *C. asiatica* common and habitats well protected.


Cape golden-moles

CONGO GOLDEN-MOLE

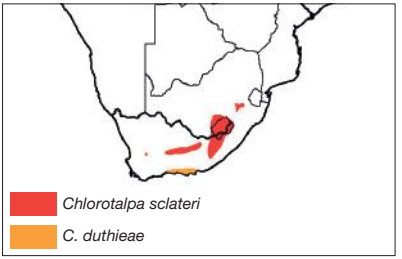
Huetia leucorhinus

MEASUREMENTS HB 63–126mm. W (est.) 15–30g.
RECOGNITION Small, grey/brown, metallic-tinted animal with an expanded, rounded back to the skull. Cranial wedge = 45 degrees. Claws: 3 = long, 2 = long and closely aligned with 3, 1 =short.
HABITAT Equatorial forest zone, both north and south of Congo R.
FOOD Invertebrates, mostly captured underground.
STATUS Rarely recorded, but widespread. Formerly in genus *Calcochloris*.


Congo Golden-mole

FORTY-TOOTHED GOLDEN-MOLES *Chlorotalpa*

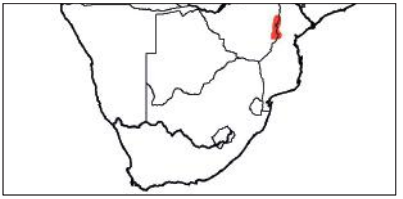
MEASUREMENTS HB 95–138mm. W 40–75g.
RECOGNITION Small, compact animals with a rounded skull. There is a metallic sheen to the generally dark fur. They have 40 teeth. Cranial wedge = 42 degrees. Claws: 3 = long, 2 much shorter than 3, 1 = very short.
SPECIES *C. duthiae*, *C. sclateri*.
HABITAT Very varied, mostly dry sandy soils in South Africa.
FOOD Invertebrates.
STATUS Wide but fragmented range; habitats well protected.



Forty-toothed golden-moles

ARENDS'S GOLDEN-MOLE *Carpitalpa arendsi*

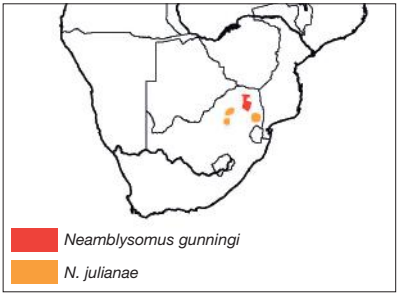
MEASUREMENTS HB 115–141mm. W 43–70g.
RECOGNITION Medium small, metallic sheen to generally very dark fur. Cranial wedge = 42 degrees. Claws: 3 long, 2 = thin and much shorter, 1 = short.
HABITAT Restricted to Manica uplands (Mozambique and Zimbabwe) in loam soils in mosaics of open and wooded, mostly montane habitats.
FOOD Invertebrates.
STATUS Locally common but thought vulnerable.



Arend's Golden-mole

LESSER NARROW-HEADED GOLDEN-MOLES *Neamblysomus*

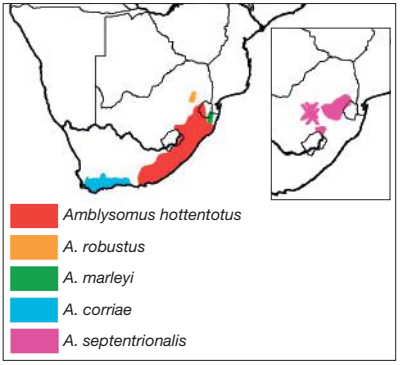
MEASUREMENTS HB 100–132mm. W 26–70g.
RECOGNITION Medium small, brown golden-moles from SE uplands of South Africa. Formerly included in *Amblysomus* but genetically distinct. Cranial wedge 50 degrees. Claws: 3 = long, slender, 2 = medium and very slender, 1 = well developed and very slender.
SPECIES *N. gunningi*, *N. julianae*.
HABITAT *N. gunningi* is known only from one montane locality. *N. julianae* is also localised in drier uplands. Moist or sandy soils in Afromontane zone and both high and low veld.
FOOD Invertebrates.
STATUS Both species are vulnerable or endangered.



Lesser narrow-headed golden-moles

NARROW-HEADED GOLDEN-MOLES *Amblysomus*

MEASUREMENTS HB 100–130mm. W 21–75g.
RECOGNITION Dark, shiny golden-moles with a long body and a small, narrow head (with 36–40 teeth). Hair bases are grey. Cranial wedge: 42 degrees. Claws: 3 = robust, 2 = shorter, less robust, 1 = short.
SPECIES *A. hottentotus*, *A. robustus*, *A. marleyi*, *A. corriae*, *A. septentrionalis*.
HABITAT Except for very localised (and endangered) *A. marleyi* and *A. robustus*, *Amblysomus* species are common and widely distributed in South Africa.
FOOD Invertebrates.
STATUS Varies from species to species.



Narrow-headed golden-moles

SENGIS (ELEPHANT-SHREWS) MACROSCELIDEA

Soft-furred sengis (Soft-furred elephant-shrews)	Macroscelidinae
Giant sengis (Giant elephant-shrews)	Rhynchocyoninae

Mouse- or rat-sized animals with large eyes and ears, slender limbs and a long, bare tail. Sengis have a tubular snout protruding from a strongly tapered skull bearing 50–60 teeth. Most species are brownish and some have bold markings on the face or back.

Modern sengis are the remnants of a larger radiation that included tiny, mouse-like herbivores (Mylomygale) which survived until 1 million or so years ago. Older, larger relatives appeared to resemble hyraxes closely and were therefore named 'Myohyrax'. Like hyraxes, some earlier herbivorous sengis probably occupied niches that are now dominated by the more advanced herbivores that have replaced them.

All living forms of sengi are specialised invertebrate-feeders (ants being particularly important) and were previously included in the insectivore 'scrap-basket'. Since 1998 sengis have been recognised as a distinctive order within the newly named Afrotheria.

Separation of the fine-boned, soft-furred sengis (Macroscelidinae) from the more robustly built giant sengis (Rhynchocyoninae) dates back 25 million to 35 million years. The former are superficial surface-gleaners of small invertebrates (and occasionally fruits and seeds) in shaded but dry environments while the latter favour moister habitats where they find invertebrates through an intensive turning-over of leaf-litter.

SOFT-FURRED SENGIS (SOFT-FURRED ELEPHANT-SHREWS) MACROSCELIDINAE

Four-toed Sengi	*Petrodromus tetradactylus*
Round-eared Sengi	*Macroscelides proboscideus*
Lesser sengis	*Elephantulus* (11 species, 4 groups)

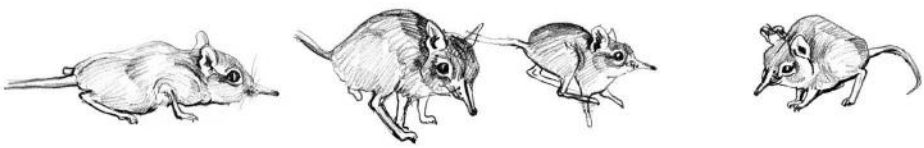
RECOGNITION Characterised by long, dense, silky fur, a mass of long, fine whiskers, a fine, narrow proboscis, naked rump and large, very dark eyes with vertical pupils. They have a relatively uniform sandy colouring (except around the eyes).

GENEALOGY Recognisable as fossils some 35 million years ago, the most distinct and conservative type is the narrow-headed four-toed sengi, *Petrodromus*. Of other sengis, *Macroscelides* is also relatively unspecialised, while the genetics and morphology of North African *Elephantulus rozeti* links the fecund radiation of *Elephantulus* with the other Macroscelidinae.

GEOGRAPHY Exclusively African, they are mainly restricted to uplands in the east, south and (marginally) north-west. They are not found in very humid habitats and their distribution is bounded by the major rivers in central Africa.

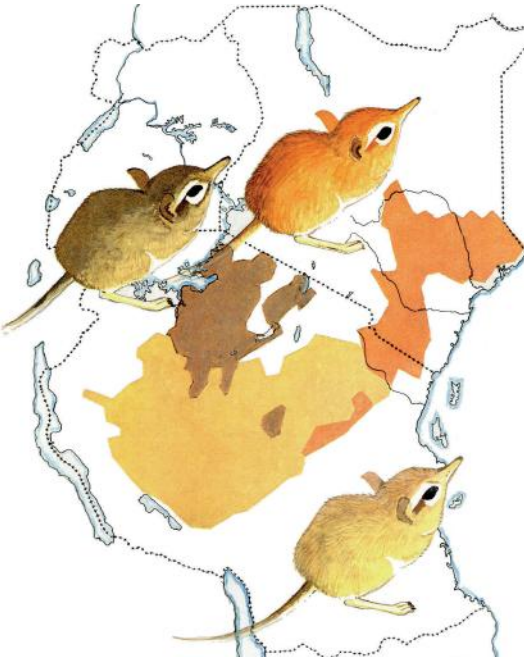
ECOLOGY Alert surface-foragers and pouncers, they are almost exclusively diurnal and mostly active while conditions are warm. The invertebrate diet is occasionally supplemented by fruits or seeds.

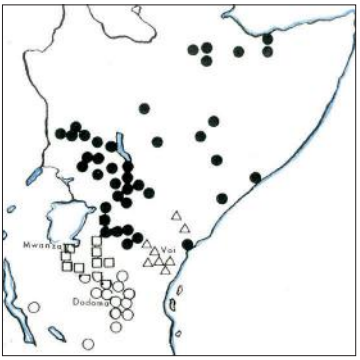
NATURAL HISTORY Soft-furred sengis mature very rapidly and have a brief but fecund adult life. Gestation may last as long as a fifth of the female's life-span. Species vary in their reliance on cover, shelter or burrows but all are exceptionally fast runners and leapers. Both males and females defend exclusive territories from their own sexes, effectively forming permanent pairs that forage and sleep on their own.



Distribution of dominant soil colours in East Africa and localised types of *Elephantulus rufescens* from Voi (red), Mwanza (grey) and Dodoma (yellow).

Local distribution map (*below*):
black circles = mildly polymorphic populations
open triangles = rufescent population
open squares = grey population
open circles = yellowish population

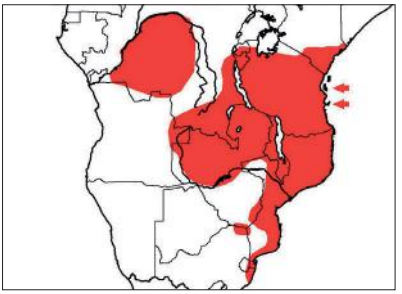




ADAPTATIONS The long, powerful hindlegs of soft-furred sengis enable them to make vertical leaps from a standing start and to sustain their rapid, bounding locomotion; these are crucial defences against their numerous predators. Coat colours often match local soil types very closely. Their long, narrow tongue enables them to gather small food items with great rapidity.

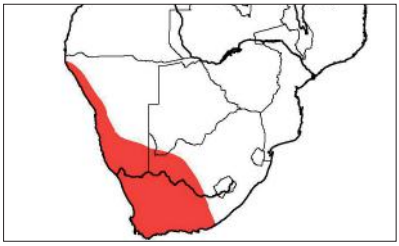
FOUR-TOED SENGI *Petrodromus tetradactylus*

OTHER NAMES Four-toed Elephant-shrew. Fr. *Pétrodrome*. Ger. *Russelrate*. Swah. *Isanje*.
MEASUREMENTS HB 165–220mm. T 130–180mm. W 150–280g.
RECOGNITION Brown, rat-sized sengi with a large head and ears and conspicuous facial markings. The legs are light-coloured and very slender, with only four toes. There are two pairs of mammae.
GEOGRAPHIC VARIATION Five subspecies described. *P. t. sultan* (from E Kenya) has, with some justification, sometimes been regarded as a separate species; it is unique in having a profusion of knob-tipped bristles growing from a glandular tract that lines the underside of the tail (see illustration).
DISTRIBUTION SE and central Africa with a distinct population inhabiting the Congo R. basin (south of the main river).



Four-toed Sengi

HABITAT Mainly in dense evergreen undergrowth in caesalpinoid forests, woodlands and thickets. The Four-toed Sengi may depend upon a complex plant/animal community that sustains a rich leaf-litter micro-fauna. It lives without recourse to burrows or shelters on the forest or thicket floor, using habitual pathways with regularly spaced 'landing pads' of cleared, bare earth.
FOOD Mainly ants and termites; also crickets, grasshoppers and other litter invertebrates.
BEHAVIOUR This sengi is most active in the early morning and evening, scuffling litter to find food. Rapping of the hindlegs is presumed to be a territorial advertisement and alarm signal. Neighbours answer with similar foot-rapping. Most young are born in the wet season at an advanced stage of development and they reach sexual maturity very rapidly. They have a wide repertoire of low-level purrs, miaows, squeaks, chirps and screams.
STATUS Intensively hunted in parts of its range but not endangered overall.



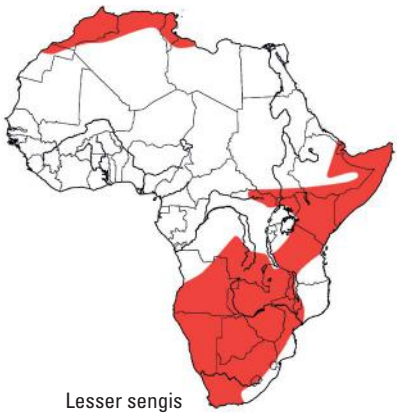
Round-eared Sengi

ROUND-EARED SENGI *Macroscelides proboscideus*

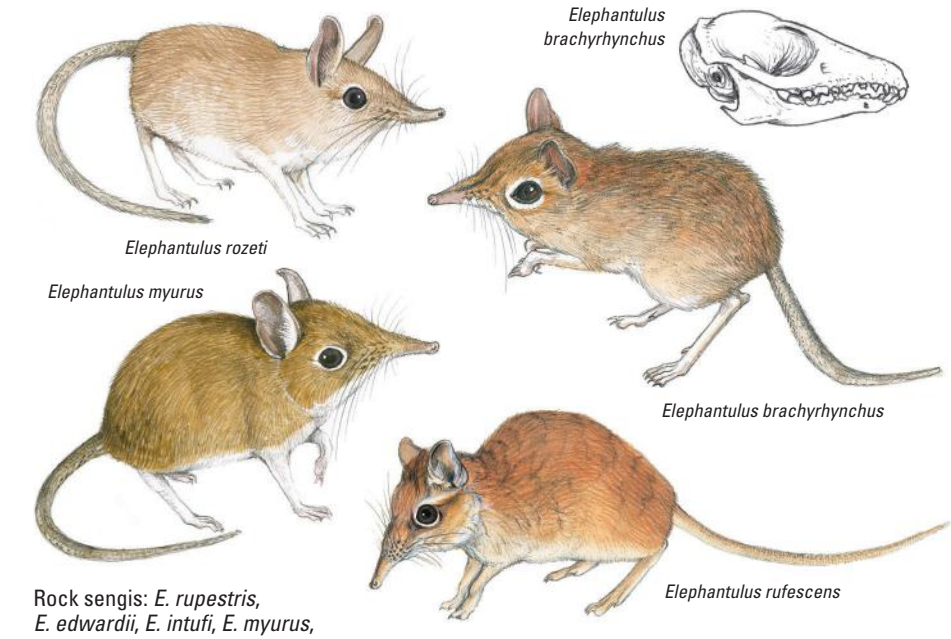
OTHER NAMES Round-eared Elephant-shrew. Fr. *Macroscélide d'Afrique du Sud*. Ger. *Russelspringer*.
MEASUREMENTS HB 105–115mm. T 114–130mm. W 31–47g.
RECOGNITION A grizzled, mouse-sized animal with rounded, hairy ears and a short muzzle. There is no ring of white fur around the eye. The skull is characterised by crowded teeth and greatly inflated ear bullae. Colour varies from grey to buff or brown. There are three pairs of mammae.
HABITAT Areas of low Karoo scrub in South-West Arid zone. Single animals or pairs live in small territories. Most births occur between September and February during warmer, wetter periods.
FOOD Ants and termites.
STATUS Widespread within its restricted habitat.

LESSER SENGIS *Elephantulus*

OTHER NAMES Elephant-shrews. Fr. *Macroscélides*. Ger. *Elefantenspitzmaus*. Swah. *Sengi*.
MEASUREMENTS TL 210–280mm. W 25–70g.
RECOGNITION Mouse-sized, soft-furred, naked-tailed animals with large eyes and ears, a fine-pointed proboscis and long hindlegs. There are rings of white or paler fur around the eyes. Some species secrete from glands on the chest, soles of the feet and sites on the underside of the tail (others secrete from one or more of these areas). Coat colour often closely matches local soil colour.
SPECIES There are four distinct subgroups:
Mahgreb Sengi: *E. rozeti* (anatomically and genetically intermediate between *Elephantulus* and *Petrodromus*).
Short-nosed sengis (formerly '*Nasilio*'): *E. brachyrhynchus, E. fuscipes, E. fuscus.*



Lesser sengis



Rock sengis: *E. rupestris*, *E. edwardii*, *E. intufi*, *E. myurus*, *E. pilicaudus*.
Lesser sengis: *E. rufescens*, *E. revoili*.

DISTRIBUTION The eastern and southern half of Africa and the extreme north-west (Morocco). Species are well defined in their geographic ranges and habitat preferences, some preferring sandy areas, others rocky or densely vegetated areas.

HABITAT Relatively dry but seasonal, bushy or scrubby habitats are preferred. All species minimise exposing themselves to predation by remaining under vegetation and rocks and only crossing open ground at high speed. Some species (*E. rupestris*, *E. intufi*) dig burrows; others (*E. rufescens*) maintain conspicuous paths that are daily cleared of litter by scuffling with the legs; yet others (*E. brachyrhynchus*) make use of vacant rodent holes.

FOOD A wide range of invertebrates, pounced upon in leaf-litter (and near the dung piles of herbivores). Some species occasionally eat fruits and seeds. Rapid daily traverses along pathways in small, well-known territories serve to exclude trespassers and rehearse rapid escape from predators. However, the main function of such runs is to gather food.

BEHAVIOUR Both males and females exclude their own sex from territories but may tolerate adult-sized offspring in home ranges of 0.25–0.6ha. Territorial displays involve fluffing out the fur and strutting on tip-toe (which displays the white or contrasting colour of the legs and underside). Very intense, rapid activity is followed by long periods of quiescence in well-concealed, shady observation posts. All species are predominantly or wholly diurnal and several sunbathe before becoming fully active. These sengis communicate with squeaky calls and by drumming the hindlegs. Most species have continuous or extended breeding, with the majority of births falling in warm, wet months.

ADAPTATIONS Being highly vulnerable to birds of prey and snakes, these sengis have extremely rapid reactions. They also minimise the vulnerable period of infancy by having a long gestation (about 2 months) and giving birth to well-developed young that reach adult size in just over 1 month and become sexually mature in 2 months. Their reproductive life of about 1 year allows no more than three litters, in which one or two (rarely three) young are born. In competition with more fecund rodents and insectivores, their intensive use of a very small, well-known area, acute observation and very fast actions compensate for a low rate of reproduction and short lives.

STATUS Favoured in areas well stocked with wild or domestic herbivores (probably due to the dependence of certain invertebrates on dung and plant litter). In general not threatened, but some species or populations may be threatened when overstocking degrades the habitat to the point where patches of shelter disappear.

GIANT SENGIS (GIANT ELEPHANT-SHREWS) RHYNCHOCYONINAE

RECOGNITION Elegant, long-legged animals the size of a large rat, with a long, naked, white-tipped tail and a very long, tapering snout. The proboscis protrudes well beyond the mouth (which is inconspicuous, as are the very rapid movements of the long, tapered tongue). The coat is short-haired and sleek. The five species differ greatly in colour but are of similar size and morphology. Their pungent smell derives from a gland behind the anus. There are no obvious differences between the sexes but females have longer, sharper canine teeth.

GENEALOGY The divergence of this group from soft-furred sengis is thought to date back 35 million years or more. They mature more slowly, live longer, forage more intensively in larger territories and live a less exposed existence than their smaller relatives.

GEOGRAPHY More exclusively tropical than soft-furred sengis, they also live in moister, denser forests and woodlands but, like other sengis, seem to have retained a long-term preference for the drier, south-eastern half of Africa and have failed to range very far to the west. Large rivers mark their present frontiers but it seems likely that very humid habitats support a complex of competitors, predators, diseases and physical conditions that have always deterred expansion into moist, western forests.

ECOLOGY Feeding on relatively cryptic invertebrates (larvae, termites, ants, beetles, spiders, myriapods and earthworms), they noisily turn over litter and soil with their paws and well-reinforced but flexible nose. They require relatively well-drained soils and abundant dry leaf-litter in order to construct their 1m-wide leaf-mound shelters, which are piled over shallow, body-sized scoops in the soil. Each animal makes and maintains 10 or more such retreats in its territory. They serve as the night-rests of these exclusively diurnal animals, as nurseries for the young and as occasional daytime refuges. Constructed in the early morning, when leaves are damp, limp and compressible (and the sound of raking and tamping them is muffled), they provide concealment from a variety of predators. The presence of the right conditions for the building of dry, comfortable leaf-mounds is possibly one of the most important requisites for giant sengis.

NATURAL HISTORY Territories average 1.7ha and are defended by each animal against others of its own sex. Females are the more frequent trespassers, provoking chases and fights in which wounds from the short, tusk-like canines are common. The entire home range is traversed daily and scent marks from the anal gland probably serve as territorial beacons. A male regularly monitors the one or more females sharing his home-range but all feeding and resting is solitary. Breeding is continuous, with four or five litters (each of a single offspring) being born in a year after a gestation of 45 days. The young remain within the leaf-mound for up to 2 weeks before emerging and becoming independent within a few days. Young animals rapidly reach sexual maturity. Giant sengis live for 4–5 years.

Large birds of prey and snakes are frequent predators but predation levels appear to be lower for this group than for soft-furred sengis, possibly because leaf-mounds are such effective refuges. The mounds are difficult to identify, even for an experienced observer, and the occupant is usually able to 'explode' out of its refuge before it can be seized. Nonetheless dogs are a serious menace for populations close to settlement.

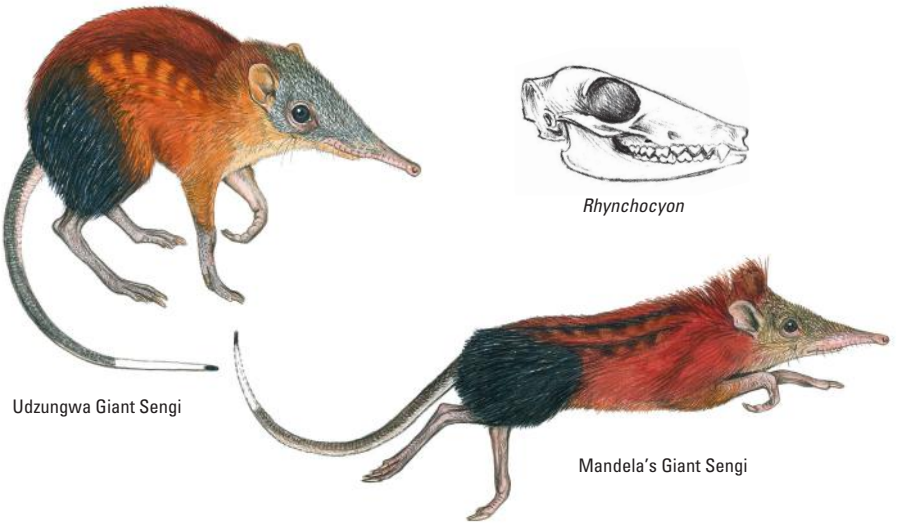
ADAPTATIONS Although less cryptic in their colouring and behaviour than their smaller relatives, giant sengis share extremely fast reactions. Instantaneous get-aways powered by well-muscled hindlegs and fast races along very well-known trails help protect both groups from predators. A broad, compressed skull and ground-hugging crouch allow these animals to occupy very little space within their leaf-mounds, where they sleep in a posture that leaves them ready for instant action. Physiologically they appear well adapted to digest toxic or difficult foods, such as ants and myriapods. However, some millipedes may be taken less frequently or avoided. That these animals show relatively little change over some 30 million years suggests that their micro-habitats, and the niches they occupy within them, must have retained a remarkable degree of stability. The IUCN Action Plan points out that *Rhynchocyon* serves as an important indicator for the health and status of forest habitats in East Africa – in this case a clear indicator of ecological stability over many millions of years.

GIANT SENGIS *Rhynchocyon*

Udzungwa Giant Sengi	*Rhynchocyon udzungwensis*
Mandela's Giant Sengi	*Rhynchocyon* sp. nov.
Golden-rumped Giant Sengi	*Rhynchocyon chrysopygus*
Black-and-rufous Giant Sengi	*Rhynchocyon petersi*
Chequered Giant Sengi	*Rhynchocyon cirnei*

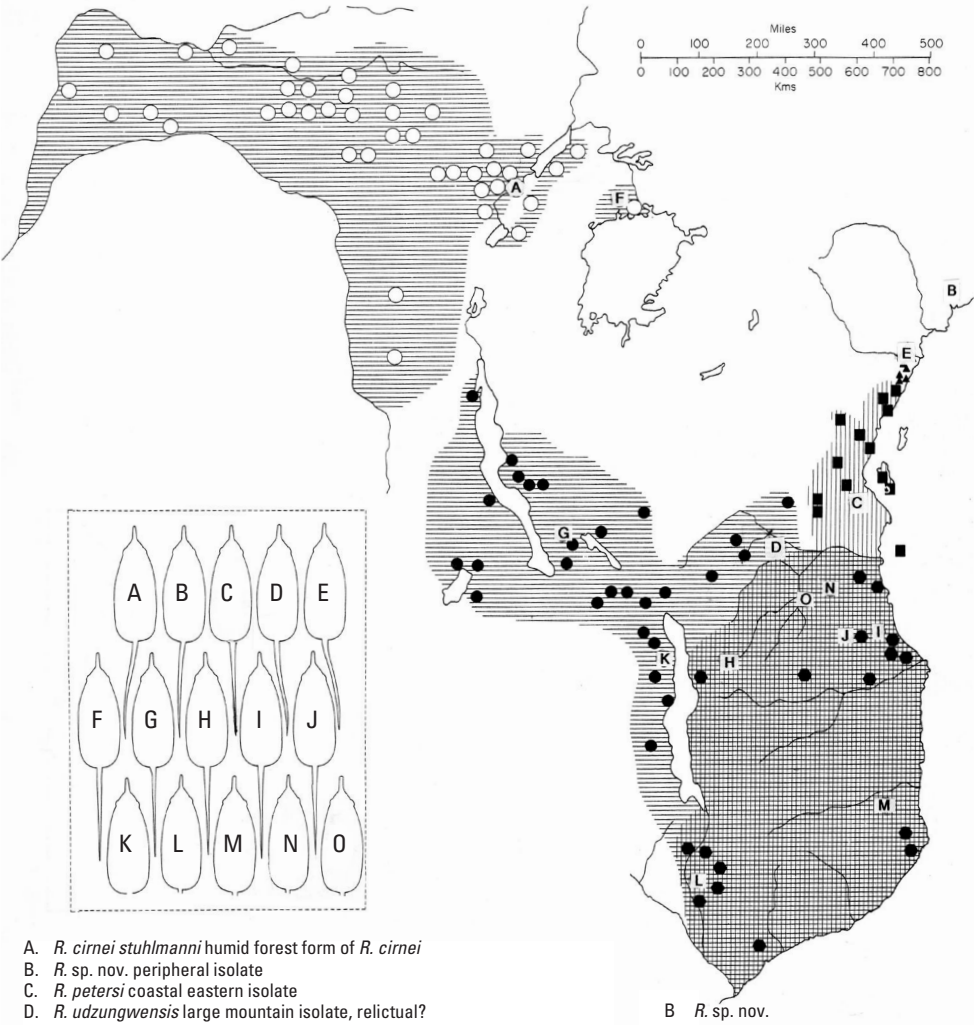
UDZUNGWA GIANT SENGI *Rhynchocyon udzungwensis*

OTHER NAMES Fr. *Rhynchocyon de Udzungwa*. Ger. *Udzungwahundchen*. Swah. *Njule ya Uzungwa*.
MEASUREMENTS HB 250–350mm. T 190–290mm. W (est.) 420–475g.
RECOGNITION Intensely black rump graduating into rich russet shoulders and thorax. Two rows of red-orange spots, of very variable visibility, are perceptible on each flank. Forehead and face greyish agouti. Tail mostly black above, off-white below, but black-tipped after conspicuous wholly white section.
HABITAT Confined to two forests in the Udzungwa Mts where it survives in spite of presence of the much more widespread and common *R. cirnei reichardi* in adjacent forests.
FOOD Grasshoppers and crickets, beetles, spiders, millipedes, ants, centipedes, earthworms and termites.
STATUS Vulnerable (IUCN). There is very serious concern for the survival of this species.



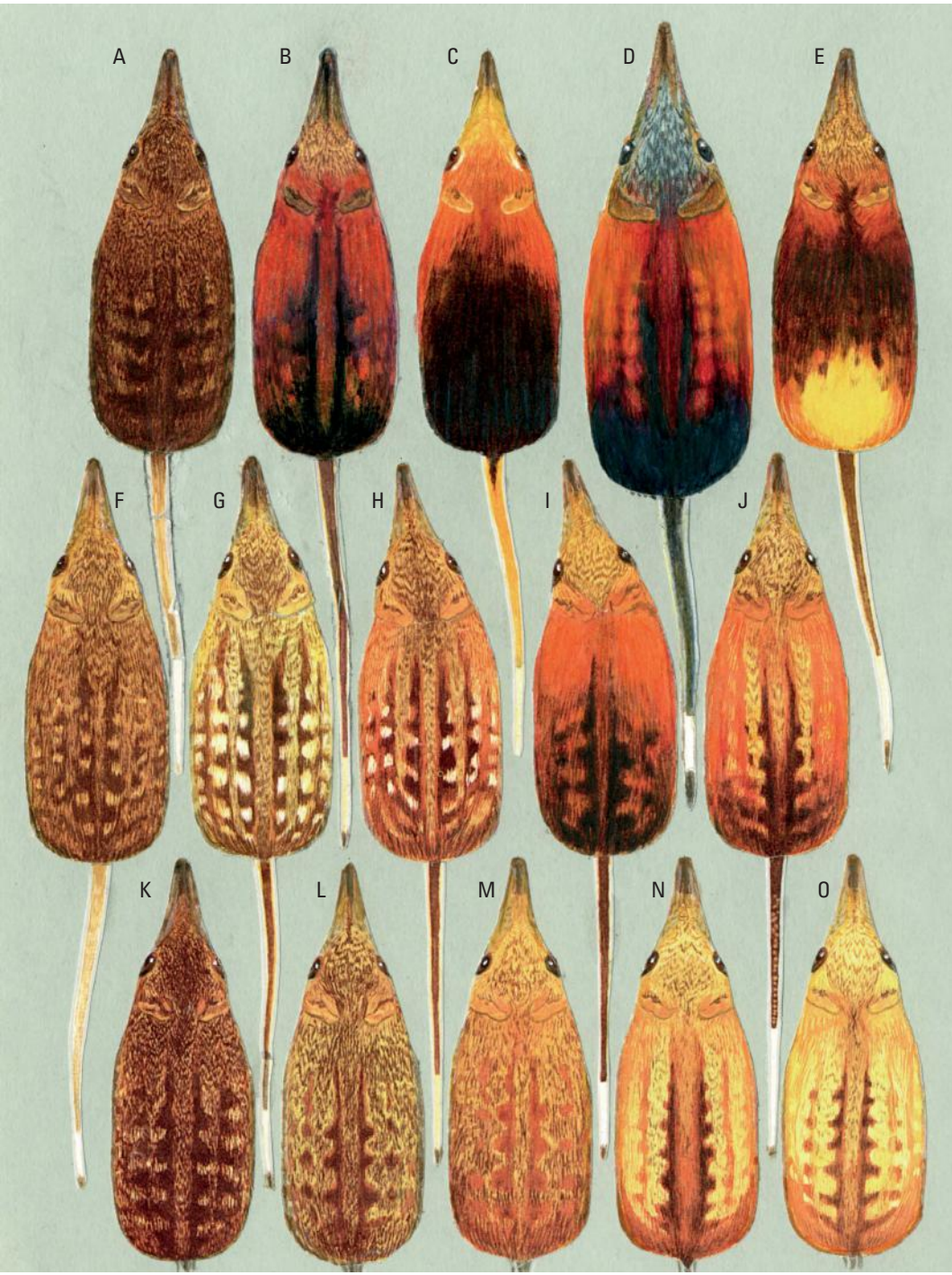
MANDELA'S GIANT SENGI *Rhynchocyon* sp. nov.

OTHER NAMES Fr. *Rhynchocyon de Mandela*. Ger. *Mandelahundchen*. Swah. *Njule ya Madiba*.
MEASUREMENTS HB (est.) 235–315mm. T (est.) 200–300mm. W (est.) 400–450g.
RECOGNITION Black rump with paired black lines along each side of a mahogany dorsal stripe that begins with a very pronounced deep red crest between the ears and tapers off before it reaches the tail; face and cheeks tawny agouti. Vestigial traces of a spotted pattern.
HABITAT Confined to the Boni and Raas Kaamboni forests, close to Kenya's coastal border with Somalia in dry evergreen thickets.
FOOD Supposedly similar to *R. chrysopygus*, ants and termites being particularly important.
STATUS The minute range of this species renders it exceptionally vulnerable to any ecological change. Its habitat straddles a border between conflicted nations, and this species has been named to honour a great African leader and peace-maker.



A. *R. cirnei stuhlmanni* humid forest form of *R. cirnei*
B. *R.* sp. nov. peripheral isolate
C. *R. petersi* coastal eastern isolate
D. *R. udzungwensis* large mountain isolate, relictual?
E. *R. chrysopygus* Kenya coastal isolate
F. *R. cirnei stuhlmanni* Uganda isolate of A.
G. *R. c. reichardi* woodland and gallery form of *R. cirnei*
H. *R. c. macrurus* = 'Mozambique polymorph' (Songea)
I. Mozambique polymorph (Lindi)
J. Mozambique polymorph (Rondo)
K. *R. c. hendersoni* dark montane form of G.
L. Mozambique polymorph (Shire)
M. Mozambique polymorph (Nampula)
N. Mozambique polymorph (Utenge)
O. Mozambique polymorph (Shuguri)

Pelage patterns and corresponding map and key of *Rhynchocyon* spp. distribution.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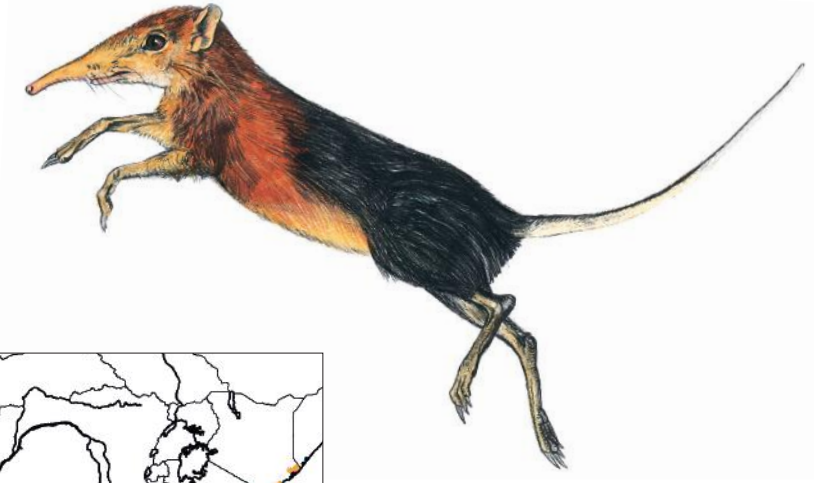
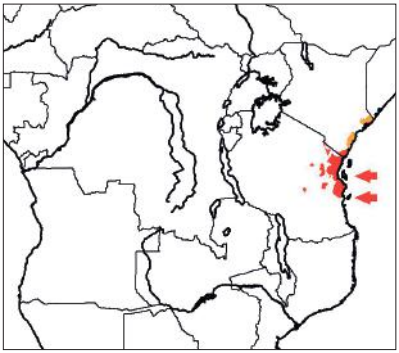
GOLDEN-RUMPED GIANT SENGI

Rhynchocyon chrysopygus

OTHER NAMES Golden-rumped Elephant-shrew. Fr. *Rhynchocyon à dos doré*. Ger. *Russelhundchen*. Swah. *Njule ya Gedi*.
MEASUREMENTS HB 235–315mm. T 190–263mm. W 408–440g.
RECOGNITION The dark body graduates to a metallic yellow rump. The neck is russet and the forehead and face are tawny agouti. Vestigial traces of a spotted pattern similar to that of the Chequered Giant Sengi are obvious in juveniles and just perceptible in some adults. Thickened skin under the golden rump suggests that damaging bites or slashes inflicted during territorial fights and flights may be targeted on this rump shield.
HABITAT Confined to two very small areas of the Kenya coast, where it lives in dry evergreen thickets.
FOOD Grasshoppers and crickets, beetles, spiders, millipedes, ants, centipedes, earthworms and termites (in order of preference).
STATUS Vulnerable (IUCN). There is great concern for the survival of this species. Domestic dogs have seriously depleted it in the Gedi NP in recent years. A vast sea-port in the vicinity may hasten its extinction.





Golden-rumped Giant Sengi
Black-and-rufous Giant Sengi

BLACK-AND-RUFOUS GIANT SENGI

Rhynchocyon petersi

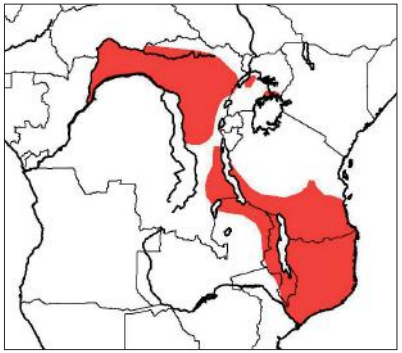
OTHER NAMES Black-and-rufous Elephant-shrew; Zanj Elephant-shrew. Fr. *Rhynchocyon de Zanj*. Ger. *Russelhundchen*. Swah. *Njule Kinguja*.
MEASUREMENTS HB 235–315mm. T 190–263mm. W 408–440g.
RECOGNITION Forequarters are orange, graduating to a deep red with a black rump. The tail is orange with a white tip.

GEOGRAPHIC VARIATION *R. p. petersi* (Mombasa to R. Rufiji), *R. p. adersi* (Zanzibar I. and Mafia).
HABITAT Coastal and montane forest and thickets in E Tanzania and the Kenya coast.
FOOD Cryptic invertebrates in leaf-litter.
STATUS Vulnerable (IUCN). Action plan proposals are to determine: (a) current range and densities; (b) use of fallow lands; (c) effects of hunting; (d) field research priorities; (e) appropriate conservation measures.

CHEQUERED GIANT SENGI

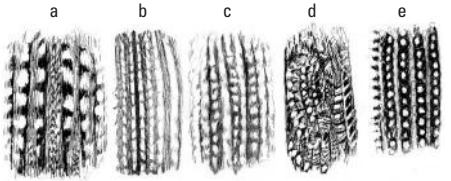
Rhynchocyon cirnei

OTHER NAMES Chequered Elephant-shrew. Fr. *Rhynchocyon*. Ger. *Russelhundchen*. Swah. *Njule madoa*.
MEASUREMENTS HB 235–315mm. T 190–263mm. W 408–440g.
RECOGNITION The back is marked with a complex pattern of longitudinal dark bands on an agouti-grizzled background with pale (even white) spots or flecks in the most consistently patterned subspecies, *R. c. reichardi*. In the humid Congo R. basin and mountains north of L. Malawi (L. Nyasa) this pattern becomes difficult to see because the overall colour is very dark. In the mosaics of moist savannas, forests and thickets in SE Tanzania and Mozambique the pattern is very variable.



Chequered Giant Sengi

GEOGRAPHIC VARIATION
Three main populations:
R. c. cirnei and allies (highly variable polymorphs between Rufiji and Zambezi rivers and L. Malawi (L. Nyasa), includes *macrurus*, *shirensis*).
R. c. reichardi (SW Tanzania and E DR Congo), includes darkish *hendersoni* from mountains around north end of L. Malawi).
R. c. stuhlmanni (NE DR Congo and Uganda).
HABITAT Forests and gallery forests at low, medium and high altitudes. *R. c. reichardi* (with colouring that closely resembles that of grass-mice, ground squirrels and other cryptic taxa) inhabits grassland during the wet season, only retreating into galleries or relict forest patches in the dry season.

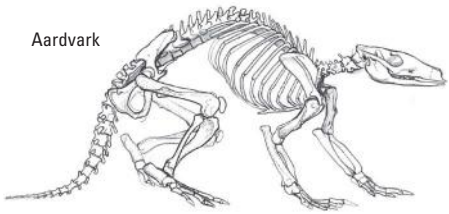


Convergences in cryptic, predator-selected patterns. a. *Rhynchocyon cirnei reichardi* (Afrotherian sengi). b. *Lemniscomys macculus* (African murid rodent). c. *Spermophilus tridecemlineatus* (American ground squirrel). d. *Caprimulgus pectoralis* (African nightjar). e. *Cnemidophorus* sp. (whiptailed lizard).

FOOD As other species, but grasshoppers and caterpillars are important for some races.
STATUS Generally not endangered (but susceptible to dogs and declining in densely settled areas).

AARDVARK TUBULIDENTATA

The modern Aardvark is distinguished by many peculiarities, notably in the teeth, which lack enamel and are composed of densely packed tubules surrounded by columns of dentine, the whole tooth being contained in a sleeve of dental cement. These peg-like molar teeth are at the back of a toothless snout (although embryos and infants have a full complement of vestigial milk-teeth, including canines). The muscles surrounding a highly mobile nose end in a hairy disc around the nostrils. This flat-fronted snout-disc represents the front of an olfactory sensor that is directed at everything an Aardvark encounters as it forages, with head swinging from side to side. Behind the snout and in front of the eyes is a swollen bulge that roofs over a balloon of turbinals, all around a very highly developed olfactory lobe. All this apparatus and behaviour represents a level of olfactory prowess with capabilities that science has yet to investigate in any depth. Although aardvarks evolved in Africa, some fossil forms indicate that they found their way to Eurasia and Madagascar.

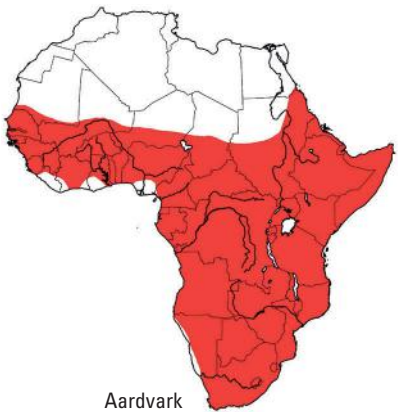

Aardvark

AARDVARK ORYCTEROPODIDAE

If one disregards the Aardvark's more obvious ant-eating specialisations (peculiar nose and teeth, digging claws, robust limbs and musculature), then its skeleton resembles various generalised mammals known from fossils, among them *Phenacodus*, a 60-million-year-old proto-ungulate. The living aardvark species replaced other, generally smaller, more lightly built aardvarks and the survival of such a large ant-eating mammal signifies extraordinary efficiency at many levels of physiology, anatomy and behaviour.

AARDVARK *Orycteropus afer*

OTHER NAMES Antbear. Fr. *Oryctérope*. Ger. *Erdferkel*. Swah. *Muhanga, Kukukifuku*.
MEASUREMENTS HB 1.0–1.58m. T 440–630mm. H 580–660mm. W 40–82kg.
RECOGNITION The Aardvark's long nose, squared-off head and tapered tail are rather delicately built extensions in comparison with the massive body and the muscular limbs, which are armed with great, nailed digits. The fur on many old individuals can become heavily abraded but young animals are well furred (short on the head, nape and tail, longer and darker on the body, especially on the limbs). The Aardvark is a shy, nocturnal animal and rarely seen. Its burrows, spade-like scratchings and tracks are more commonly seen than the animal itself.


Aardvark

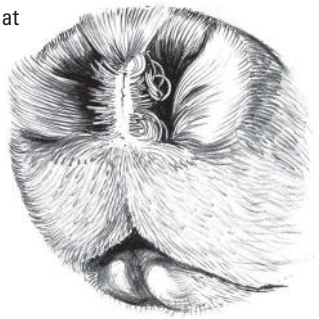
GEOGRAPHIC VARIATION Eighteen subspecies have been named but most, if not all, are invalid due to substantial yet little-studied variation. The snout in particular is subject to differences in proportions and angle. The Aardvark is normally rare or absent in rainforest.
DISTRIBUTION A large part of sub-Saharan Africa with past extensions down the Nile valley and Hoggar/Tassili Mts.
HABITAT Patchily distributed in areas with a year-round abundance of ants and termites and beetle larvae. The earth that is preferred for digging warrens may be at some distance from foraging areas, so nightly walks between the two are normal in some localities. Very hard or stony soils and regularly flooded areas are avoided. In highly stratified hills the Aardvark may select a particular stratum for its more regularly used warrens. These may be occupied mainly by females and their young as males are thought to be less sedentary. Temporary 'camping' holes of only a few metres in

Aardvark

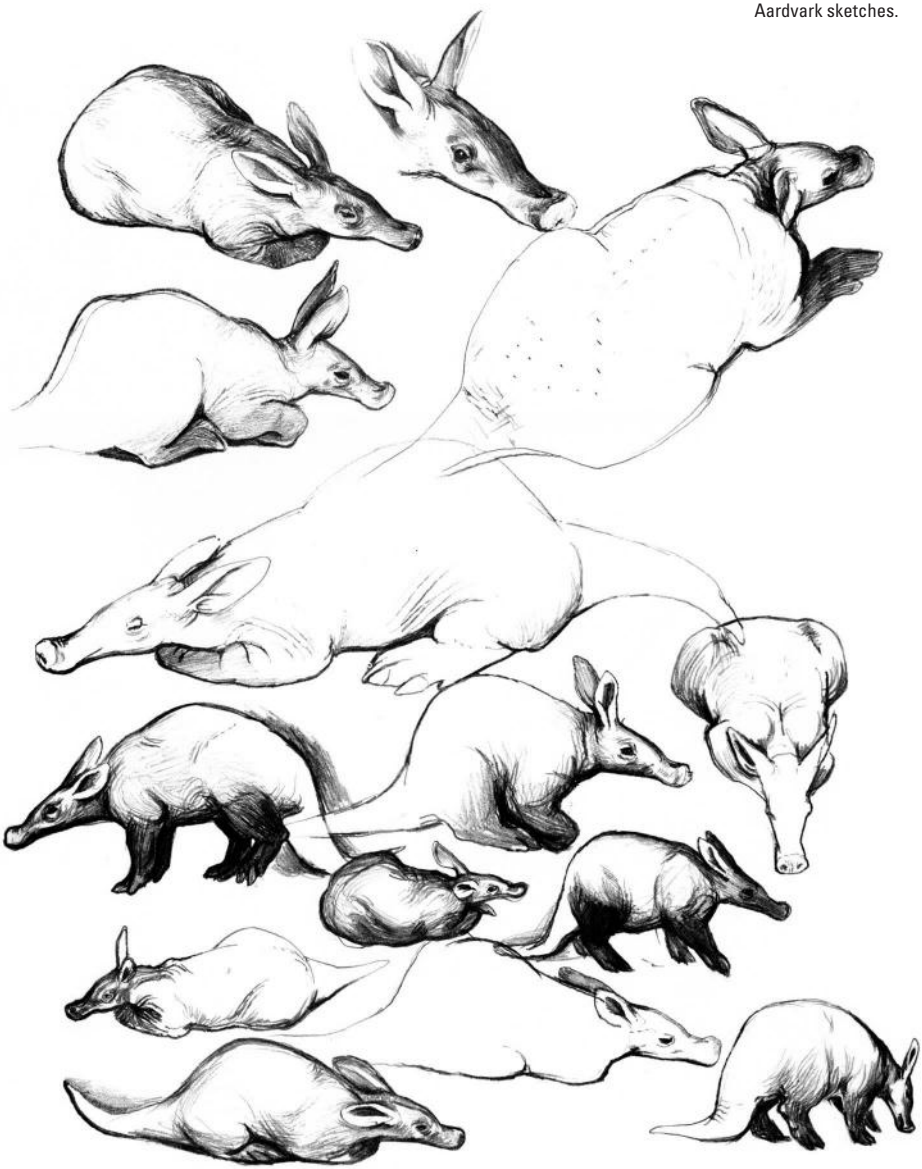
length are more frequent than the much longer warren complexes, which can have eight or more entrances and descend as deep as 6m. Entrances are normally plugged, sometimes with a 'vent' left open at the top of the plug. With its spade-like claws the Aardvark can dig with great force and speed in suitable soils.

FOOD Termites, ants and larvae are foraged for at night, beginning an hour or two after dusk. Most food is found on or very close to the surface but subterranean termitaries, ants' nests and beetle caches may be extensively excavated. However, the colonies of social insects are seldom entirely destroyed (the deterrent is probably a critical concentration of defending soldiers). Termites that live on or very near the surface are *Hodotermes*, *Odontotermes*, *Microtermes*, *Pseudacanthotermes*, *Trinervitermes* and *Macrotermes*. During periods and in localities where ant colonies outnumber or are more available than termite colonies, these may become the principal diet. Recorded ant prey are *Anoplepis*, *Camponotus*, *Crematogaster* and *Dorylus* but very many more genera are also taken. Scarabeid pupae or larvae are likely to come in similar seasonal or local bonanzas. It is gluts of termites, mainly in the wet season, that are likely to fuel seasonal deposits of fat in the Aardvark. Insects are swept into the small mouth by the long, sticky tongue and are swallowed with little or no chewing. As at least one fossil aardvark species appears to have had no teeth, the function of teeth in living species may be quite marginal. Insects are processed in the pyloric region of the muscular, gizzard-like stomach.

BEHAVIOUR Normally solitary. Female Aardvarks are accompanied by one, occasionally two, young (of different ages). Where Aardvarks are very common and large warrens well established, they may be used by more than two or three animals. Males' genitals secrete a powerful musk and both sexes have glandular areas on the elbows and hips. These presumably help with the spacing of individuals and with mating but ostentatious scent-marking has not been observed. The only recorded sounds made by an Aardvark are a grunt and, in extreme fear, a bleat. One, rarely two, young are born after a gestation estimated at 7 months. Born naked but with open eyes, they begin to follow the mother after 2 weeks and start eating insects at 3 months, becoming independent at 6 months and sexually active at about 2 years. The Aardvark lives for up to 18 years.



ADAPTATIONS The sense of smell is greatly refined by a structure that vastly increases the turbinal surfaces (which help to process olfactory signals). These are minutely convoluted bones and tissue that radiate from the olfactory lobes of the forebrain, visibly swelling the middle profile of the skull. Also linked with locating hidden food are thick, fleshy tentacles on the septum of the nose (which may function like the appendages of the North American Star-nosed Mole). The snout itself is not at all pig-like, being soft, mobile, rounded and furry, with dense hair around the nostrils (detail right). Swollen upper lips completely conceal the small mouth



Aardvark sketches.

below. The sides of the face and the tail are pale-coloured or white in females, darker in males, colour differences that may help young to locate or follow their mothers.

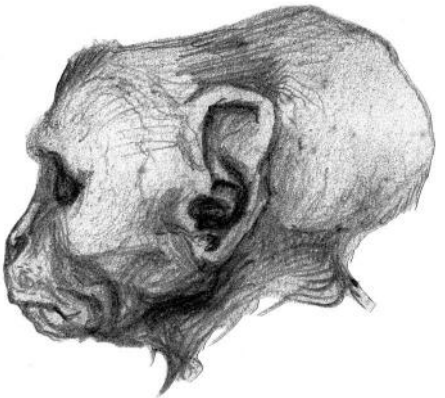
STATUS The Aardvark is still widespread but has been widely exterminated in many agricultural areas. This is mainly because of hunting but many farmers and ranchers destroy the animals because their holes are inconvenient or dangerous to vehicles, stock and water dams. Cultivation tends to eliminate their food supply. Extermination has extensive side-effects because Aardvark holes are extremely important as refuges for many species of small mammals, including bats and carnivores, and also reptiles and birds. The Aardvark is vulnerable in all settled areas and endangered or extinct in many other localities.

Old World monkeys, apes and humans	Catarrhini
Prosimians	Strepsirrhini

All primates derive from, and to some degree retain, a primitive body plan that they share with other unrelated arboreal mammals, such as squirrels, tree-shrews and possums. The common arboreal condition is long-backed and short-necked, with five-fingered, clinging hands and feet. The forearms are linked to the chest by collar bones (clavicles) and the compact head has forward-oriented eyes and a short, flexible neck.

A great diversity of anatomical specialisations has developed in primates and these correspond to different climbing or locomotory techniques. Relatively slow, careful climbers have developed extreme mobility in their limb joints and a powerful grip in their hands and feet. Fast branch-runners have long tails to serve as balancers, long, flexible backs, limbs with narrow hands and fingers, small thumbs and well-developed bifocal vision to help them accurately assess distance and space.

Judging from tooth structures in fossils, the arboreal mammals that gave rise to primates were mainly insectivorous. The earliest extensions in diet would have been small vertebrates and ripe, soft fruits. Later, some tackled unripe or hard fruits, resins, flowers, nectar, buds, young leaves and, finally, a few took on mature leaves, which are very difficult to digest. From very early times up to the present, omnivorous primates might have been able to eat small quantities of any of these foods and insect-eating has remained important for many species. Trends towards consuming larger quantities of abundant but more difficult foods (such as old leaves, resins, hard nuts and seeds) led to early specialisation in lineages such as colobus monkeys and gum-eating galagos (bushbabies).



Infant Patas Monkey *Erythrocebus patas*. Typical signs of paedomorphism are a diminished face and an enlarged brain.

The commonest, most versatile and probably earliest type of locomotion consists of running and walking on four limbs of approximately equal length. This can be modified for both tree- and ground-dwelling (with marked elongation of the limbs in the more terrestrial forms, such as Patas Monkeys and Savanna Monkeys). The most economic and efficient locomotion in open woodlands and forests, where there are abundant vertical stems or trunks, is fast, frog-like springs powered by extremely long hindlegs. Galagos show varying degrees of this trait. By contrast, lengthening of the forelimbs is typical of the apes. Best developed in the Asiatic gibbons, which are true brachiators, this trait is correlated with shortening of the trunk into a more compact, barrel-like body.

Powerful big toes are known to have developed in fossil primates by at least 60 mya. Thumbs have a less certain ancestry and are less universal (some primates, notably colobus species, have lost them altogether). Naked, padded digits and palms on both hands and feet are universal and clearly represent one of the very earliest adaptations of primates, a fact that has a direct bearing on human evolution.

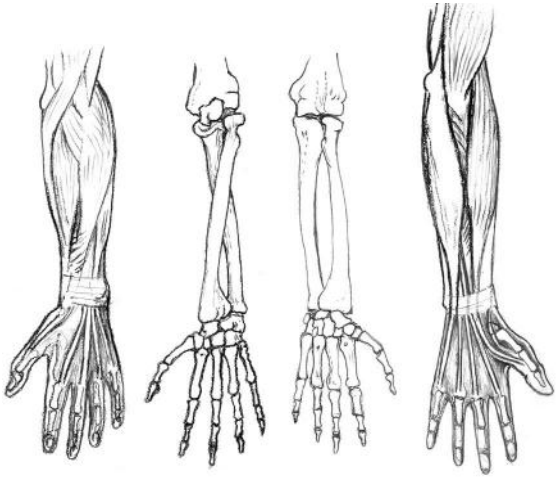
Decline in the sense of smell seems to be associated with the superiority of touch and vision as means of exploring and surviving in a frequently rain-washed world of three-dimensional space latticed by branches. Where muzzles are large or long, as in mandrills and baboons, this seems to be linked with enlargement of the bony anchorage for powerful sets of teeth.

Fossils reveal that a more forward orientation of the eyes had developed by about 60 mya. This narrowing of the field of vision seems to have been compensated for by greater ability to rotate the head on a very short neck. Efficient rotation is helped by a compact, round head. A tentatively dated phylogenetic tree for the radiation of primates demonstrates the great age of primates as well as how recently humans have evolved.

OLD WORLD MONKEYS, APES AND HUMANS CATARRHINI

Anthropoids	Hominoidea
Old World monkeys	Cercopithecoidea

Shortening of the face seems to be linked with an ancient convergence of the nostrils into a single nose unit and an enlargement of the upper lip. This enlargement has allowed muscles to spread into the upper lip, assisting manipulation of food but also enhancing facial expressions and vocalisations. Such enhancement has proceeded furthest among anthropoids, as has brain enlargement. South American primates diverged from their African counterparts between 50 and 40 mya. It is presumed that their ancestor crossed a then narrow Atlantic on a floating island of African forest trees.



Pronation and supination of the human hand is made possible by rotation of the ulna and radius.

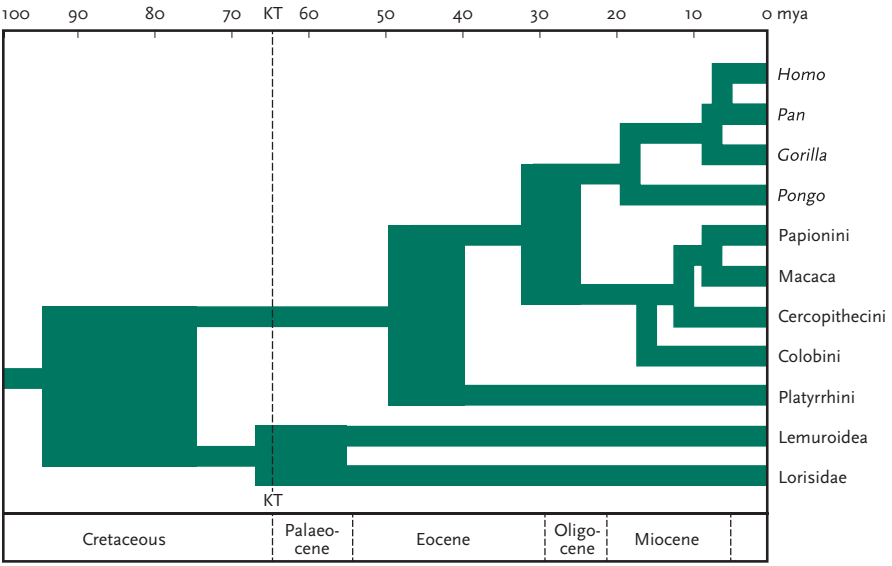
APES AND HUMANS HOMINIDAE

Gorillas	*Gorilla* (2 species)
Chimpanzees	*Pan* (2 species)
Hominins	Hominini

African apes are so frequently illustrated and filmed, and captives are so familiar in zoos, that a formal description of apes may seem superfluous. There have been bland scientific descriptions dating back more than 300 years. All tended to suppress human resemblances and stressed the similarity of apes to one another. All failed to anticipate the extraordinary discoveries of the past few decades. Study of fossils, genes, physiology and behaviour has revealed that the common ancestry of humans and apes is much more recent than anyone thought possible and human evolution has been confirmed as a mainly African story.

By the rules that govern the classification of other animals, both apes and humans have had to be united in a single group: the anthropoids or hominids. In this entirely new perspective the differences between chimpanzees and gorillas become as significant and interesting as their similarities, as do their subtly different ecologies. This is particularly so when it is appreciated that chimpanzees are more closely related to humans than they are to gorillas. Thus it is that many international teams of scientists are studying and comparing chimpanzees with humans, with the ultimate objective of revealing the roots of our own uniqueness.

We all share compact, tail-less bodies, large, rounded, big-brained heads and long forearms with hands and strong fingers. In apes, both hands and feet share the three main functions of body support, climbing and manipulating objects. For human ancestors this last activity, foraging with the hands for small food items, became their primary speciality. The skeleton of a nearly 5-million-year-old fossil 'Ground Ape', *Ardipithecus*, was described for the first time in 2009. The broad, flat feet of this hominid suggest that they served as a firm platform for foraging on the ground. Thus it was *hands* that drove hominin evolution. Looking at other primates and other mammals, there are innumerable other examples of physical transformation linked with similar small shifts in function. Our most obvious peculiarity, developing two-handed skills, is paralleled by the clawless

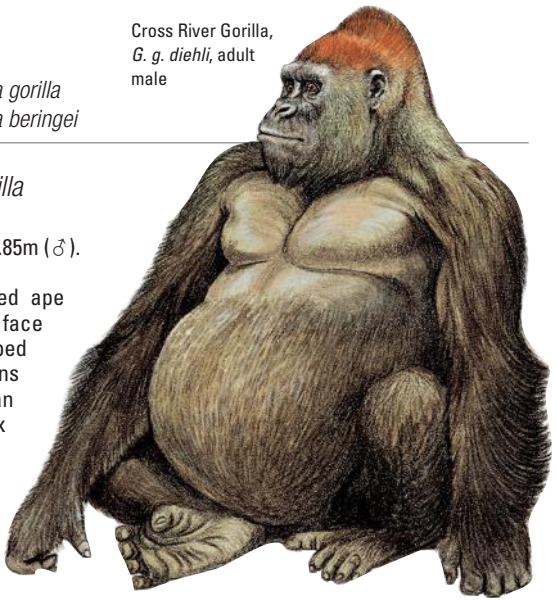


Tentative composite phylogenetic tree for African primates (assembled from Steiper & Young 2006, Bininda-Emonds *et al.* 2007, Janečka *et al.* 2007).

otters and the Marsh Mongoose, while such diverse mammals as the springhares, the Ground Pangolin and the Gerenuk have all found advantages in regular two-footedness. Like us, all these species have become very different from their closest relatives simply by evolving novel ways of using their limbs. In our case, hand-use was closely linked with brain-use, but it is important to remember that most of our two-legged ancestors had brains no bigger than those of chimpanzees. Palaeontologists have revealed that at least 15 varieties of bipedal hominins existed over the last 6 million years. Their appearance can be reconstructed from known fossils. Why none has survived remains a mystery.

GORILLAS *Gorilla*

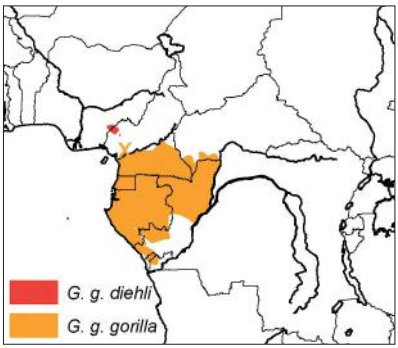
Western Gorilla	*Gorilla gorilla*
Eastern Gorilla	*Gorilla beringei*



Cross River Gorilla, *G. g. diehli*, adult male

WESTERN GORILLA *Gorilla gorilla*

OTHER NAMES Fr. *Gorille.* Ger. *Gorilla.*
MEASUREMENTS SH 1.3–1.5m (♀), 1.4–1.85m (♂). W 58–72kg (♀), 145–191kg (♂).
RECOGNITION Very large, barrel-chested ape with relatively even hair, a bare black face and chest, and small ears. The bar-shaped brows are joined and the nostril margins are raised. Females are smaller than males. Coat colour varies by region, sex and by age but generally brownish.
GEOGRAPHIC VARIATION
Western Lowland Gorilla, *G. g. gorilla* (W Nigeria to Congo R./R. Sangha): brownish with a broad face but relatively small jaws.



Western Gorilla

Cross River Gorilla *G. g. diehli*, adult female and infant

Western Lowland Gorilla *G. g. gorilla*, adult male posturing in lateral 'head and shoulder display'

Cross River Gorilla, *G. g. diehli* (W Nigeria and SE Cameroon): brown with a shorter, smaller head but broader face than *G. g. gorilla.*

DISTRIBUTION Extends from the Cross R. to Congo R./R. Sangha. A relict western population survived until the turn of the century at Bondo on the R. Uelle.

HABITAT Found in lowland tropical rainforest; in W Africa they inhabit mixed tropical rainforest where fruits play a large part in the diet and the animals frequently climb trees to feed. They co-exist with chimpanzees over most of their range but eat a much more diverse range of foods, a possible implication is that Western Gorillas have a substantially longer tenancy in these forests.

FOOD The Western Lowland Gorilla eats more fruits than the Eastern species but also relies on wild ginger (*Afromomum*) for a high proportion of its diet.

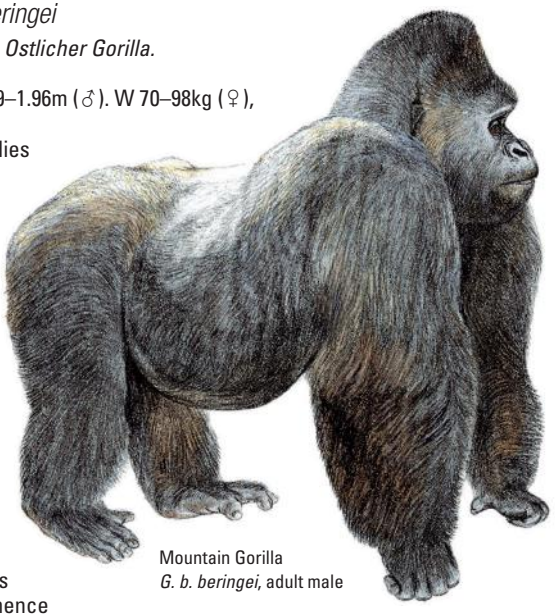
BEHAVIOUR Animals form small, non-territorial harems dominated by a single, mature male. Male offspring are driven out and females not infrequently change groups. The Western Lowland Gorilla seldom forms groups with more than three adult females (average five in all; maximum 12). The commonest call bears some structural resemblance to chimpanzee hooting. It is a crescendo of deep, booming hoots, culminating in a tattoo of chest-beating (this can be heard over 2km away on a clear day). Various degrees and conditions of alarm are signified by barks, roars or screams, almost all made only by the male. Females and young are quiet and retiring. They have a modest repertoire of grunts, burps, growls and whines.

Gorillas reproduce at a very slow rate, on average one young every 4 years (a maximum of about 10 in a female's lifetime). Mothers give continuous care and attention to their young. The dominant male continuously defends all members of his group.

ADAPTATIONS While females bear some superficial resemblance to chimpanzees, males are by far the largest living primate and appear to be conscious of their power, expressed in ostentatious postures and noisy charges against intruders, whether conspecific or not.
STATUS In areas where agriculture is expanding, gorillas are killed in retaliation for crop-raiding. The secondary growth that follows large-scale logging may temporarily favour them but rapid expansion of the commercial bushmeat trade means that gorilla meat is sold in markets and restaurants in several central African towns as well as exported out of Africa, as are the living orphans of this trade. Gorillas are declining fast in most parts of their range, partly through recent exposure to disease. West Africans have yet to develop initiatives such as gorilla-watching, which has transformed communities (both human and gorilla) in Uganda and Rwanda. The Western Lowland Gorilla is listed as critically endangered (IUCN).

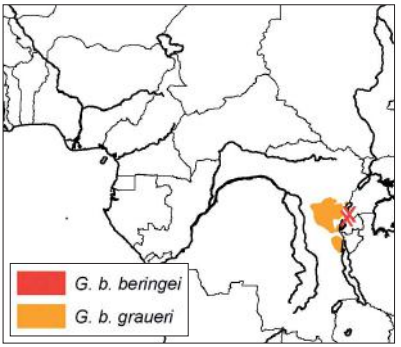
EASTERN GORILLA *Gorilla beringei*

OTHER NAMES Fr. *Gorille de l'Est.* Ger. *Ostlicher Gorilla.* Swah. *Makaku, Gorila.*
MEASUREMENTS SH 1.6–1.7m (♀), 1.69–1.96m (♂). W 70–98kg (♀), 120–209kg (♂).
RECOGNITION Recent genetic studies have shown that Eastern and Western Gorillas are as distinct from each other as Common (Robust) Chimpanzees and Bonobos (Gracile Chimpanzees), in spite of greater superficial resemblance between the gorilla species. Eastern Gorillas are very much more terrestrial and blacker in colour; populations living in the mountains have long, dense hair, especially on the arms. The females are smaller than males. The belly of wild Eastern Gorillas is very much more massive than in captive specimens. The small of the back, or 'saddle', of mature males becomes grey or white with age, hence the name 'silverback' for old males (although aged females may also become grey).



Mountain Gorilla
G. b. beringei, adult male

GEOGRAPHIC VARIATION
Mountain Gorilla (Eastern Mountain Gorilla), *G. b. beringei* (volcanic slopes of Virunga Mts): very black and densely furred, with a broad face and massive jaws.
Grauer's Gorilla (Eastern Lowland Gorilla), *G. b. graueri* (Rift wall and lowlands of E DR Congo): short black fur, narrow face and very large body size. (Gorillas from Bwindi forest in Uganda could be a third race.)
DISTRIBUTION Occupy a triangular wedge between the R. Lualaba (Congo R.), L. Edward and L. Tanganyika.



Eastern Gorilla

HABITAT *G. b. beringei* is confined to mountain and subalpine environments. In most other areas Eastern Gorillas prefer old clearings, old forest burn-offs, valley bottoms, landslides, etc., where there is a dense tangle of ground-level herbaceous growth.
FOOD Compared with lowland gorillas, Mountain Gorillas eat fewer plant species and feed mainly

on leaves, shoots and stems; *Galium* vines, wild celery and three or four other species make up a high proportion of the diet.

BEHAVIOUR Eastern Gorillas maintain long-term stable groups with up to five females and at least one mature male. Friction among females is rare and usually elicits an intimidating male intervention which terminates the incident. Where there is more than one adult male there is a loose hierarchy. Adolescents of both sexes tend, eventually, to leave their natal group. Both sexes become more and more attracted to the dominant male as they mature (nonetheless some young males are sometimes actually driven away) and females not infrequently change groups. A single female tends to gravitate to a solitary adult male and such primary pairs display strong bonds (adult females seldom bond closely with other females). Whenever established pairs are joined by other adult females the sequence of arrival seems to influence whatever female rank order may exist. Eastern Gorillas have less exclusive groups than Western Gorillas and a dominant 'silverback' male may tolerate several other adult males. Sometimes these larger groups may attract more females. Groups average 10 but can reach as many as 37 individuals.

An abundance of fast-growing food permits large groups to forage together (something that is rarer in most W African habitats). There is no defence of the home range and the ranges of all groups overlap those of their neighbours quite extensively. More than half the day is spent foraging. Eastern Gorillas tend to behave like ruminants, with very long rest periods. Mutual evasion between groups is facilitated by frequent vocalisations and chest-beatings emitted by the dominant male. On occasions when neighbouring males fail to evade one another, there are displays of roaring, chest-beating, plant-bashing and charging. Very occasionally these culminate in a fight. Similar displays greet human intruders, predators and competing herbivores (such as Giant Hogs or buffalos). Chest beating is frequent, can be performed by an animal of any age or either sex and occurs in many situations. Chest-beats appear to advertise that the signaller is a gorilla: the audience may well include species other than gorillas. Chest-beating apart, females and young are quiet and retiring. Like the Western Gorilla, they have a modest repertoire of grunts, burps, growls and whines.

Eastern Gorillas live for at least 45 years. Females breed all year round. The gestation period is about 255 days. Twins are rare and seldom survive for very long. The average interval between births is about 4.5 years. Female menstrual cycles range from 20 to 39 days with ovulation at mid-cycle and peak receptivity for up to 4 days: in captivity oestrous females and adult males sometimes use their fingers or palms to masturbate. Unlike chimps, there are no external signs of oestrus. A dominant male is always alert and willing to defend his group against all-comers. He may deter danger by briefly lying in ambush, or making a charge while his group escapes.

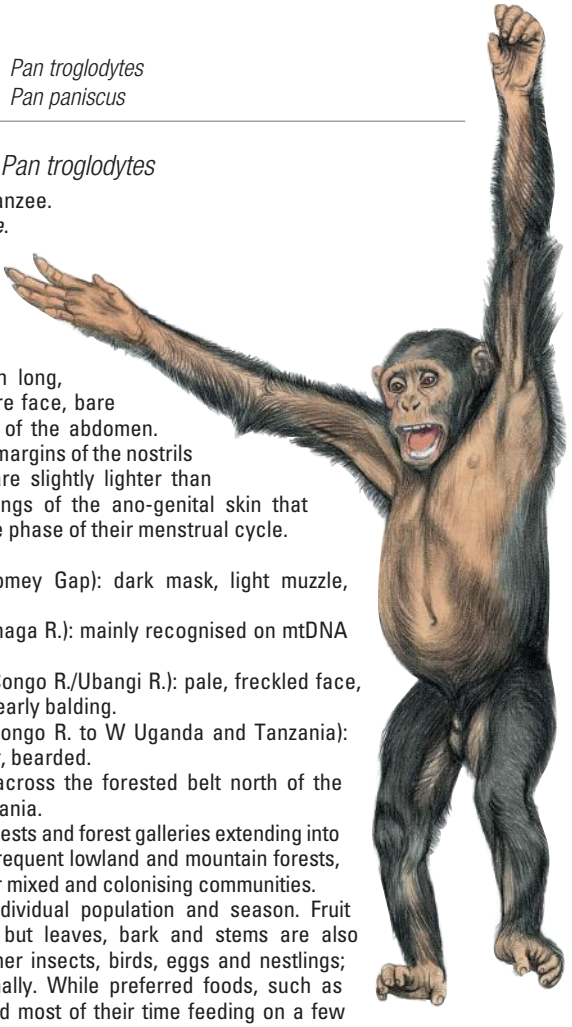
ADAPTATIONS Male defence against predators permits Eastern Gorillas to live more safely on the ground than any other primate. Their mass is less apparent in captive specimens, which eat much less bulk food. Wild males often have paunches that hang almost to the ground and the rib-cage and pelvis are correspondingly splayed. Because they spend less time in the trees and more on the ground, their hands and feet are correspondingly broad and stub-fingered.

STATUS In central Africa more than 90% of Eastern Gorillas' recent habitat is now fields and surviving populations live in lands that were, until recently, marginal for agriculture. The takeover of what remains has been delayed because of a dawning realisation that walking amongst wild gorillas is one of life's greatest privileges and an experience for which people from all over the world will pay handsomely. Gorillas have morphed from terrible cartoons of sub-humanity into a living and noble expression of humanity's roots in nature. Peasants from one of the most brutal killing fields in history now enjoy a level of well-being and contact with the outside world that was almost unimaginable when this guide was first written. They owe their new-found prosperity and access to education to dedicated naturalists and scientists who persevered, and sometimes died, to convince global audiences that allowing gorillas to go extinct would dishonour humanity. Television programmes and feature films have demonstrated how accessible habituated gorillas can be to humans, but contact brings with it the risk of disease epidemics. In spite of much local progress, most Eastern Gorilla populations continue to decline and remain endangered (IUCN).

CHIMPANZEES *Pan*

Common Chimpanzee	*Pan troglodytes*
Bonobo (Gracile Chimpanzee)	*Pan paniscus*

COMMON CHIMPANZEE *Pan troglodytes*



OTHER NAMES Robust Chimpanzee. Fr. *Chimpanzé*. Ger. *Schimpanse*. Swah. *Sokwe mtu*.

MEASUREMENTS HB 635–900mm. SH 1,000–1,790mm. W (av.). 30kg (♀), 35kg (26–40kg) (♂).

RECOGNITION A robust ape with long, somewhat tufted black hair, bare face, bare prominent ears and bare parts of the abdomen. The brows are rounded and the margins of the nostrils are scarcely raised. Females are slightly lighter than males and develop pink swellings of the ano-genital skin that fluctuate in size according to the phase of their menstrual cycle.

GEOGRAPHIC VARIATION

P. t. verus (W Africa to Dahomey Gap): dark mask, light muzzle, darkening with age, bearded.

P. t. ellioti (Dahomey Gap to Sanaga R.): mainly recognised on mtDNA evidence.

P. t. troglodytes (Sanaga R. to Congo R./Ubangi R.): pale, freckled face, darkening with age, and shows early balding.

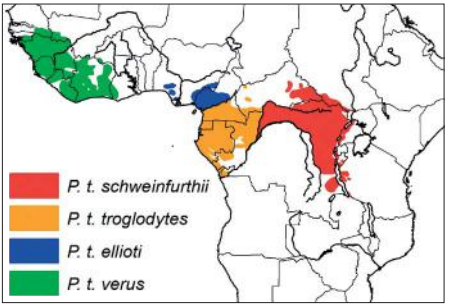
P. t. schweinfurthi (Ubangi R./Congo R. to W Uganda and Tanzania): light to dark face, dense dark fur, bearded.

DISTRIBUTION From S Senegal across the forested belt north of the Congo R. to W Uganda and Tanzania.

HABITAT Predominantly in rainforests and forest galleries extending into savanna woodlands. They also frequent lowland and mountain forests, showing a marked preference for mixed and colonising communities.

FOOD Omnivorous. Varies by individual population and season. Fruit comprises about half the diet but leaves, bark and stems are also important. Eats termites and other insects, birds, eggs and nestlings; small mammals taken occasionally. While preferred foods, such as figs, are fruiting, they may spend most of their time feeding on a few species. At other times they may be forced to forage widely, taking up to 300 different food types, as many as 20 in a single day. Where Common Chimpanzees overlap with Western Gorillas a substantially smaller range of foods are taken. One possible implication is that gorilla ancestors had a long head-start in adapting to the region while ancestral chimps entered these forests later.

BEHAVIOUR Form social communities of 15–120 animals within large territories defended by both sexes (but mostly by males). Only females cross community boundaries. Groups vary in composition and size according to the seasonal distribution of food. All-male parties, single mothers with offspring and mixed groups are common but males may forage on their own for



Chimpanzee

West African Chimpanzee

Eastern Chimpanzee

Central African Chimpanzee

Bonobo

short periods. Home-ranges are smaller in mixed rainforest, larger in forest mosaics and open savanna, i.e. 5–400km^2 (average 12.5km^2). Adult males are fiercely intolerant of counterparts in neighbouring groups and occasionally kill solitary individuals or small groups (including females and young) close to the community's territorial boundary. Strong male associations within group.

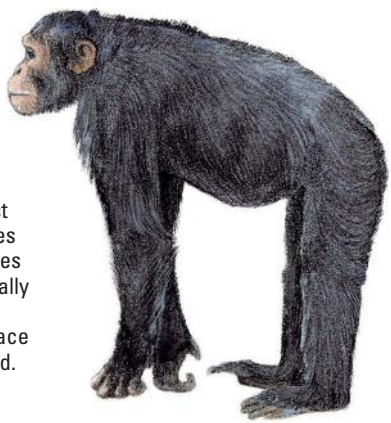
Immigrant oestrous females are generally accepted but their offspring may be attacked or killed. Non-breeding females with young offspring evade other chimps and tend to live within separate, contracted home-ranges. This preference breaks down when females come into oestrus (3–4 years after giving birth or following the death of their infant). At this time females wander more widely and excite intense male interest. Temporary pairs may form during the week in which females are at their most sexually receptive.

Common Chimpanzees feed most actively during the earlier part of morning and evening; they rest during the heat of the day. At dusk each adult and subadult animal builds a nest by pulling in, snapping and interweaving the branches that surround the chosen nest-site. Nests are normally between 6 and 25m above ground and usually built close to a final feeding site. Short-term day-nests are most typical of the wet season.

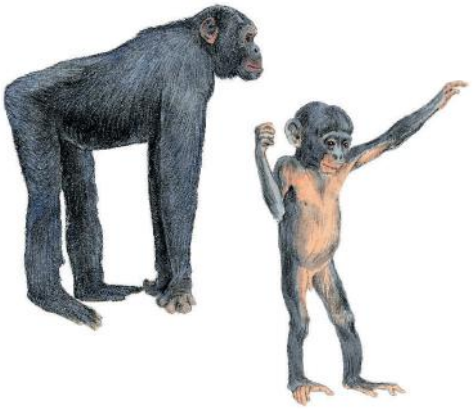
Adult males cooperate in hunting monkeys (particularly red colobus monkeys and baboons), young antelopes and pigs. Hunting often opportunistic but can display rapid mobilisation and cooperative specialisation in roles, i.e. blockers, chasers and ambushers. Sticks and stems are dipped into termite, ant and bee nests, and both clubs and rocks are used to break open nuts (and, apparently in one instance, to kill a Giant Pangolin). Common Chimpanzees communicate with more than 30 calls, which convey information about mood, status, danger, sexual excitement, food and various social interactions. Facial expressions sometimes suggest almost human levels of subtlety but may also be part of very loud and active social displays.

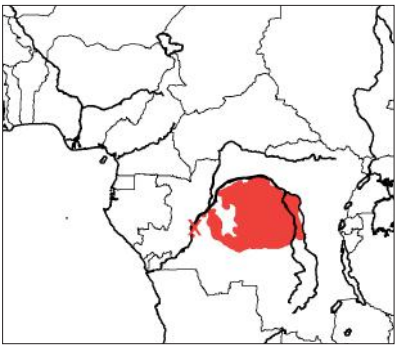
Females become fertile at about 11–12 years of age. Their sexual cycle of approximately 24 days is marked by swelling of the pink ano-genital skin. This reaches maximum extension for about a week and the swelling attracts maximum sexual interest from males at this time. Although females only give birth at about 13 years of age this has been preceded by some 4 or 5 years of sexual activity. Likewise males are only sexually mature at about 15 years but are sexually active at least 10 years before that, and males initiate most sexual activity. Gestation is 8 months, followed by birth of infant with open eyes and a strong clinging reflex but otherwise completely dependent on the mother for 6 months or more.

ADAPTATIONS The anatomy shows a fine balance between fast quadrupedal activity on the ground and the need to manoeuvre a large, heavy body through different levels of the forest on very variably sized supports. Thus, Common Chimpanzees can mount large tree trunks with spread-eagled, hugging movements that require a very powerful grip in both hands and feet and more subtle manipulation of fragile supports, such as stems, lianas and small branches. Fast travel on the ground is always quadrupedal; long strides taken on sole of foot and knuckles of hand. Short distances often covered with bow-legged, bipedal waddle, especially when arms occupied with carrying fruits.



STATUS The four subspecies have different ranges and face different threats. IUCN rates all subspecies as endangered.

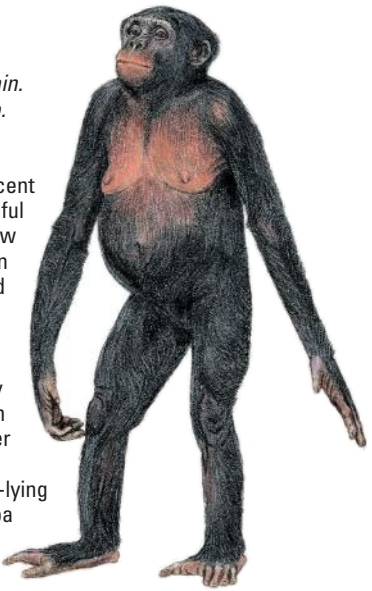




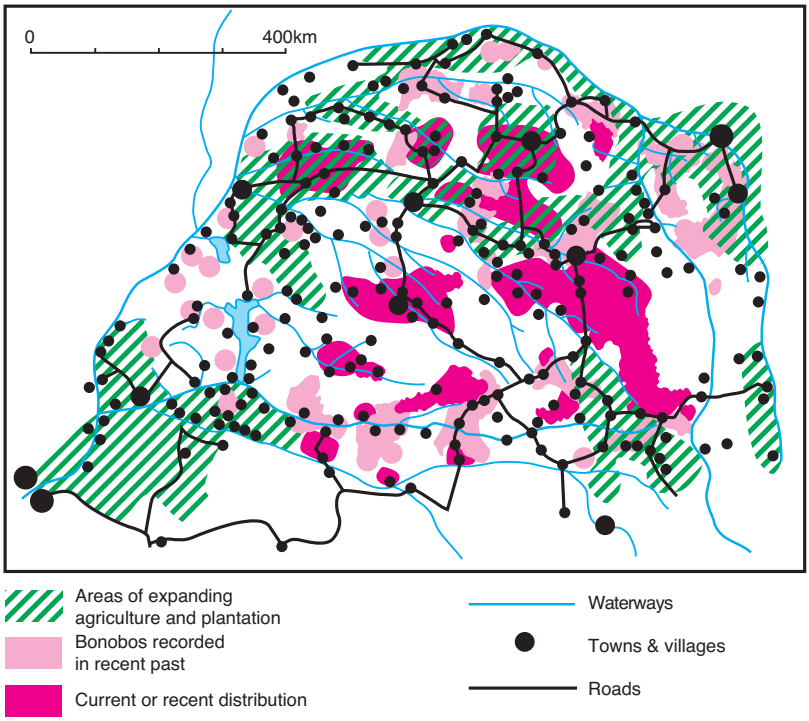
Bonobo

BONOBO (GRACILE CHIMPANZEE) *Pan paniscus*

OTHER NAMES Pygmy Chimpanzee. Fr. *Bonobo, Chimpanzé nain.* Ger. *Bonobo, Zwergschimpanse.* Lingala dialect *Mokomboso.*
MEASUREMENTS HB 700–830mm. SH 900–1,000mm. W 30kg (27–61kg).
RECOGNITION A large and beautiful chimpanzee, juvenescent rather than pygmoid. The more obvious of its numerous youthful characteristics are a rounder cranium, less pronounced brow ridges and muzzle, and less tendency to go bald. Hair on the scalp is splayed and flat while that on the cheeks and chin is heart-shaped and surrounds a black face with pink-edged eyes and lips. All limbs, especially the legs, are long and fine, their slenderness emphasised by sleek, tight fur. The narrow foot opposes an enlarged 'thumb'. There is very little difference in size between the sexes. Like the unbroken voices of human youths, Bonobos' calls are higher and weaker equivalents of those uttered by Common Chimpanzees.



DISTRIBUTION Today the Bonobo occurs only within the low-lying riverine basin enclosed between the Congo R., R. Lualaba and R. Kasai/R. Sankuru. It is probable that this ape once inhabited most of the southern Congo basin but it now occupies a diminishing scatter of pockets within an increasingly settled region. It appears to have been progressively eliminated from most settled areas and from the immediate hinterlands bordering major rivers. In some localities it may be naturally absent or scarce.
HABITAT A mosaic of swamp, primary and secondary forests in a landscape of very mild relief, with a humid, stable climate. Leguminous trees, particularly Caesalpinaceae, such as *Brachystegia, Cynometra*, *Dialium*, *Julbernardia* and *Baibiaea*, are dominant species and important sources of food. A single Bonobo community has a small core area but can range across 20–60km^2 of forest, with extensive overlaps between community ranges.
FOOD More than half the diet comprises fruits and seeds. Also eat leaves, flowers and various other plant parts, also mushrooms, invertebrates, small vertebrates, honey and eggs. Salt needs may be met by eating swamp grass (*Ranalisma*). Some 150 foods are currently known but a few species, notably velvet tamarind (*Dialium*), a liane (*Landolphia*) and soap-berries (*Pancovia),* fruit super-abundantly and are staple foods for periods of a month or more. Main feeding bout in morning, usually fruits. In afternoon may switch to lower-preference foods.
BEHAVIOUR Some differences from Common Chimpanzees can be related to the Bonobo's greater environmental affluence; for example, competition for food is much reduced during frequent gluts of fruits. Other differences derive directly from the extension of juvenile traits in both sexes. Thus



males remain close to their mothers up to adulthood, delaying male–male contacts. Prolonged subordination also results in general inhibition of male aggression towards females. Juvenescence of the loud calls further diminishes male dominance by toning down threat displays. Male aggression is further dampened by prolonged 'adolescent sterility' and sexual receptiveness in females. Juvenescence of female sexual cycle (typically longer and more irregular than in adults) lengthens the average menstrual cycle to 46 days. For nearly half of this time her attractiveness is evident in her behaviour and in her distended sexual skin. Females with young are also sexually active for 3–4 years of the 5-year gap between births. They remain infertile, like adolescent females, until their offspring are weaned, whereupon they come into full oestrus. During this period their behaviour is analogous to that of adolescent Common Chimpanzees in their close and frequent association with both sexes. When parties converge on a rich feeding site, potential antagonisms are dissipated by very frequent sex involving every combination of age, sex and status. Mutual sexual stimulation by females is frequent and it is quite usual for both homo- and hetero-couples to copulate face to face. This diversion of reproductive behaviour to social ends suggests that seduction has overtaken male dominance as the main regulator in Bonobo society. Either sex will initiate copulation. Courtship in the Bonobo is more tentative and gentler but more frequent than in any other primate.

Concentrated fruits attract all members of a regional community (up to 80 animals) but they are usually more dispersed. Females are more gregarious. All-male clusters are rarer and less stable.

Where food is plentiful only a third of the day is spent feeding. Afternoon rests and early retirement (at about 17.00) involve construction of flimsy day-nests and more robust night-nests. Although nests commonly close to current feeding site, Bonobos prefer flexible, multi-branched *Leonardoxa* trees to nest in. All reachable fronds are drawn into a wedging fork and stamped on to form a springy, globular platform.

ADAPTATIONS A narrowed choice of abundant and highly concentrated foods promotes living at higher densities. More social contacts in less competitive settings have favoured many of the behavioural traits described above. Some of these can be described as neoteny, or 'retention of youth'.

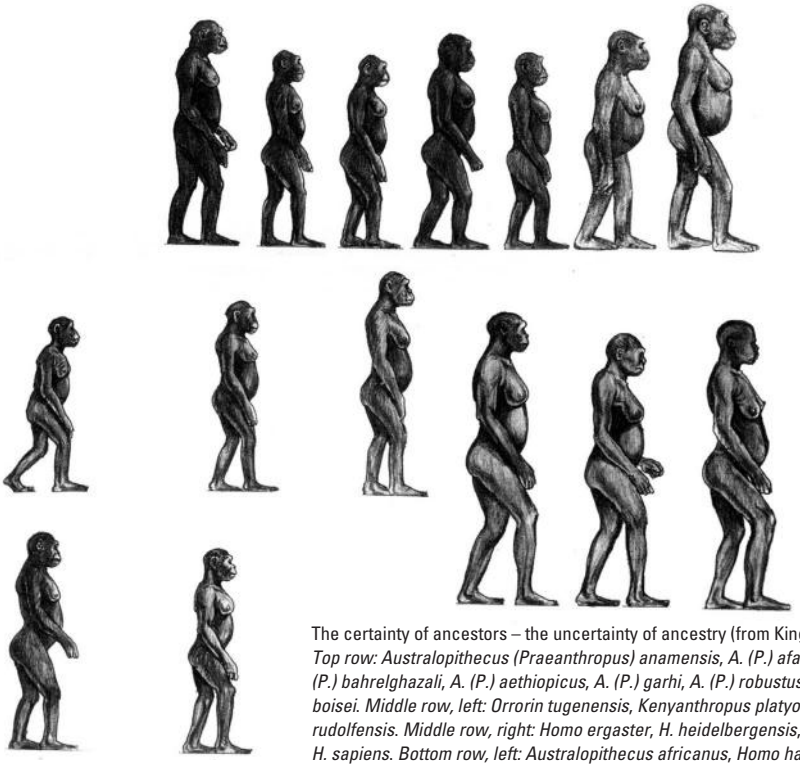
STATUS 'If the Bonobos are there we will eat them' is an oft-repeated assertion of Mongo people

in the Congo basin. This brief statement sums up the plight of the Bonobo. Formerly not all Mongo ate Bonobos but tastes and taboos change and the most pervasive changes followed colonialism. The principal large-scale economic activities in central DR Congo are logging, and coffee, rubber, cocoa, oil-palm and cotton plantation. For more than 100 years such industries have diverted traditional hunting into a commercial trade to supply workers with a year-round supply of meat. Such commercialisation long ago extended to markets in virtually every town and village. As people and their transport systems have expanded, and as hunting techniques have improved, vulnerable species have been the first to decline. The slow-breeding, conspicuous and large-bodied Bonobo is easily killed and is a favourite quarry of both subsistence and commercial hunters. This progression has only been modified in the immediate vicinity of primate research stations where scientists might have influenced attitudes or coincidentally chosen study sites in culturally benign regions.

The Bonobo's rapid decline can only be slowed if commercial hunting is arrested and both local and international industries actively support rather than subvert conservation. In Salongo, the only National Park in its range, the Bonobo is relatively scarce. Other formal refuges have been proposed but need much greater support to be effective. The Bonobo breeds well in captivity but there are fewer than 100 registered in 11 zoos. Numbers in experimental laboratories and irregular collections are unknown. Listed as Class A (African Convention), Appendix I (CITES), highly vulnerable (IUCN).

HOMININS HOMININI

Hominins emerged as the eastern isolate of an ancestral ape lineage that gave rise to both gorillas and chimpanzees in the equatorial forests of the west. Early hominins were probably omnivorous and spent significant time foraging for small food items on the ground. Fossils from this early phase are called 'ground apes', *Ardipithecus*. At this stage the principal means of subsistence was skilful excavation, manipulation and capture of food with the hands. Eventually these subsistence-



The certainty of ancestors – the uncertainty of ancestry (from Kingdon 2003). *Top row: Australopithecus (Praeanthropus) anamensis, A. (P.) afarensis, A. (P.) bahrelghazali, A. (P.) aethiopicus, A. (P.) garhi, A. (P.) robustus, A. (P.) boisei. Middle row, left: Orrorin tugenensis, Kenyanthropus platyops, Homo rudolfensis. Middle row, right: Homo ergaster, H. heidelbergensis, H. sapiens. Bottom row, left: Australopithecus africanus, Homo habilis.*

related uses of the hands outweighed their role in supporting the body and climbing. Becoming bipedal was eased by ground apes having already adopted an upright stance while foraging in a seated position. Thus hands can be identified as the principal drivers of hominin evolution and hominins became common and widespread animals within many African ecosystems. The survival of many mammals in Africa contrasts with widespread extinctions on other continents; this may well have been influenced by African species having had some 6 million years or so to adapt to hominins. Early forms were probably confined to eastern forests, woodlands and woody riverine strips. Later forms had a wider ecological and geographic range. Even allowing for much individual variation, many species evolved and more than 20 fossil species have been named. No African landscapes have escaped the presence of hominins at some time during the last few million years. Some representative reconstructions are pictured on the previous page.

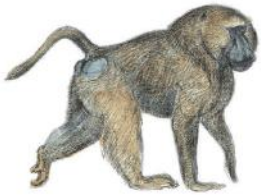
Reconstruction of face of ground ape *Ardipithecus*.

OLD WORLD MONKEYS CERCOPITHECOIDEA: CERCOPITHECIDAE

Colobus monkeys	*Colobinae*
Cheek-pouched monkeys	*Cercopithecinae*

With the exception of nocturnal bushbabies and their allies, and the great apes, all African primates are cercopithecoid monkeys. Within the family Cercopithecidae there are two main groupings: the colobines, or 'thumbless monkeys', with long limbs, large bodies and small heads, and the 'cheek-pouched monkeys', which are a more diverse group. Cheek-pouched monkeys range from the miniature talapoin monkeys and numerous colourful guenon monkeys, to the stocky, large-headed baboons.

Thumbless monkey: red colobus



Cheek-pouch monkey: baboon

All African monkeys derive from a common ancestral group, probably the extinct 'Victoria monkeys' (*Victoriapithecus* and allies). Fossils dating from a long hot period between 20 mya and 15 mya have been found at sites associated with arid-adapted fauna. In all moister habitats apes were the dominant primates of that period. The parting between the colobine and cheek-pouched monkey lineages was between 14 and 17 mya. By 10 mya colobines appear in the fossil record in Africa, Asia and Europe. By extrapolation from modern species and tooth structure, it appears that their first specialisation centred on diet. They could safely extract nutrients from indigestible parts of plants (stems, unripe fruits and leaves). Semi-terrestrial, arid-adapted Victoria monkeys had long abandoned the moist arboreal environments of all early primates but some of their descendants, whose lines eventually gave rise to the colobus monkeys, led a return into true forest. This niche probably opened up to them because apes could digest only the easier types of plant material, such as shoots and ripe fruits.

Those descendants of Victoria monkeys that remained omnivorous heightened their adaptations to a dry, open-country, mostly south–east realm; they developed cheek pouches, substantial differences in the sizes of females and males, and polygynous social groups. Large numbers of primates foraging for sparse resources in open terrain must compete intensively for all but the most abundant foods. With danger from both predators and other monkeys, cheek pouches provide an ingenious solution. Holding as much as a full stomach, they serve the same function as a shopping basket at a bargain sale: they can be crammed rapidly and the contents dealt with later. For adult males foraging in large, exposed groups, winners are the biggest, best-armed and most impressive fighters. Males with enlarged canines and body sizes are typical of all open-

country cheek-pouched monkeys. Differences between the sexes relate both to male competition and group defence.

Cheek-pouched monkeys occupy all habitats except the Sahara but are most diverse in forested areas. Colobus monkeys, although they probably originated in south-eastern Africa, now occur only in the tropical forested belt. The evolutionary shift from arid environments back into forests occurred much earlier in colobines than in cheek-pouched monkeys. Some of the latter are still savanna species but many, notably drills, mangabeys and most guenons, have become true forest species.

Activity patterns of colobus and cheek-pouched monkeys differ radically, with the former, like ruminants, spending the middle of the day totally inactive or asleep.

Terrestrial and arboreal monkeys have different limb proportions: hindlimbs are longer in the latter and more evenly balanced in the former. Early monkeys, colobines and apes all have broad faces and boldly reinforced, well-separated orbits. Cheek-pouched monkeys have the eyes closer together, in a narrowed, thinner-margined, more singular structure. Stomach structures differ, in that colobines have developed sacculations analogous to the rumen of ruminants.

COLOBUS MONKEYS COLOBINAE

Olive Colobus	*Procolobus verus*
Red colobus monkeys	*Piliocolobus* (10 species)
Pied colobus monkeys	*Colobus* (5 species)

RECOGNITION Colobus are medium-sized, variously coloured monkeys with big bodies and small heads. Some are black, or black and white; some have red tints, some have dull olive colouring. At close quarters their most distinctive peculiarity is a lack of a thumb. Amputation of the thumbs is a mutilation for humans, hence the monkeys' anthropocentric name, from the Greek *colobe,* meaning 'cripple'.

GENEALOGY A resemblance between colobus and gibbon faces is frequently noted and is best explained by a common *lack* of specialisation in their skulls and heads. It is also a resemblance that shows how conservative Old World higher primates can be in one feature while developing specialisations in another. The main colobus specialisation is hidden in the chemistry and physiology of their digestive tracts.

Nonetheless, their thumblessness does disclose two primary adaptations that would have separated colobines from other Old World monkeys by at least 11 mya and probably earlier. Only in monkeys that had become wholly committed to living in dense forest would the hands become modified into flexible hooks. This involved the alignment of the long fingers into a single, narrow, curved arc (where a thumb would actually obstruct its branch-gripping function). Because their hands have lost the ability to manipulate isolated 'droppable' objects or living prey, colobus monkeys prefer to take material off a plant directly into the mouth. Thus thumblessness confirms that colobines became wholly arboreal and wholly vegetarian at an early date.

The small Olive Colobus is a relatively primitive species that has a less demanding diet of easily digested buds, flowers and soft, young leaves. Red colobus monkeys are also conservative, requiring about half of their intake to be young digestible growth. Pied colobus monkeys are less constrained by the quality of their diet because they survive periods of shortage on drier, more mature herbage. They are the most recently evolved, having taken plant processing that much further than the other species.

GEOGRAPHY Dietary limitations in the different colobus species are reflected in their distribution and their status. The Olive Colobus is a relict species confined to the forests of West Africa. A much wider scatter of populations shows that red colobus monkeys once ranged all over the forested parts of Africa. However, much regional differentiation shows that their present, very scattered distribution is of long standing while wide gaps prove that they have been poor dispersers. Pied colobus monkeys, on the other hand, are a widely distributed and successful group. Among them the Guereza Colobus has made the most recent expansions in range and had colonised the cool montane forests of E Africa by at least 2 million years ago.

Although some Asian colobines spend much time on the ground, African species rarely leave the trees and no contemporary species occurs beyond the main outliers of Africa's tropical and montane forest belt.

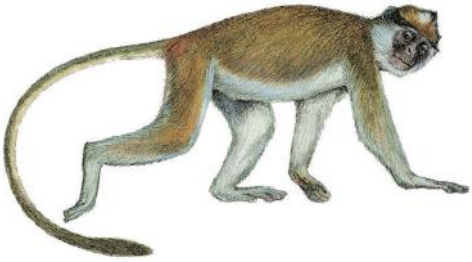
ECOLOGY A prominent part of most colobine diets consists of leguminous plants, the leaves and fruits of which are exceptionally well protected by chemicals. Because of this peculiar chemistry,

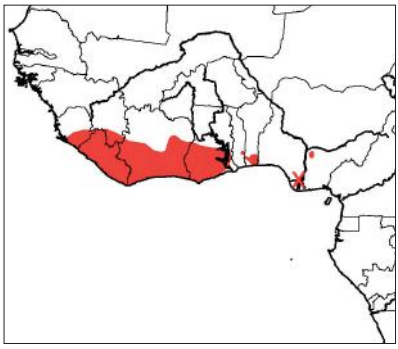
and because legumes have dominated African forests, the processing of legume toxins must have been an important factor in the evolution of colobine digestion. Difficulties in breeding captive specimens could therefore be influenced by this history of co-evolution between African colobines and leguminous trees.

NATURAL HISTORY Simplistically portrayed as leaf-eaters, the colobus monkeys are more accurately described as processors of difficult plant materials. These include fruits, seeds and petioles, as well as leaves, but colobines avoid ripe, soft and colourful fruits, preferring unripe, green or brown fruits, seeds or seed pods. All species include the latter in their diet but there are significant differences between species in the proportions of fruits and seeds that they eat: the Olive Colobus takes only between 9% and 18%, red colobus species about 30%, for the King (Western Pied) Colobus and Angola Colobus fruits and seeds make up about a third of the diet, while the proportion exceeds 50% for the Black Colobus. Reasons for this reliance on seeds may lie in a consistent scarcity of nutrients in the foliage within the Black Colobus's ancestral range. It has developed a specific preference for the seeds for which its incisor teeth are appropriately enlarged. The Guereza Colobus, though, has small incisors; it does not need to rely on seeds because its digestion can extract nutrients from hard, old leaves. This enables Guerezas to survive the long dry seasons typical of north-east Africa.

ADAPTATIONS That colobines have abandoned an omnivorous diet is further confirmed by the structure and chemistry of their complex, sacculated stomach which holds one-third of their body weight in food and requires long rests to allow digestion. This involves a process of bacterial fermentation that is similar to that of ruminants and other herbivorous mammals.

This form of digestion has developed to break down the cellulose that strengthens plants, and to detoxify the compounds that protect leaves and seeds. Deep jaws, powered by heavy cheek muscles, and large salivary glands are further colobine adaptations. The most external manifestation of colobine adaptations are disproportionately large, heavy abdomens, long limbs, small heads with square faces and long, 'acrobatic balancer' tails.





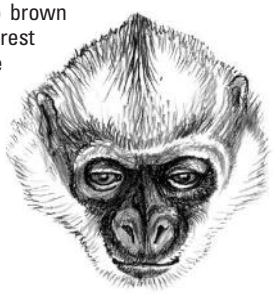
Olive Colobus

OLIVE COLOBUS *Procolobus verus*

OTHER NAMES Van Beneden's Colobus. Fr. *Colobe de Van Beneden.* Ger. *Grüner stummelaffe.*

MEASUREMENTS HB 430–500mm (♀ and ♂). T 570–640mm. W 3.0–4.5kg (♀), 3.3–5.7kg (♂).

RECOGNITION The smallest of the colobus monkeys, cryptically coloured, with a dull grey underside and greenish-olive upperside, graduating to brown on the back. The small, rounded head is distinguished by a short crest running down the crown with a light grey whorl on each side of the forehead. The hairless, dark grey face is framed by a dull-white ruff.



DISTRIBUTION Discontinuous from S Sierra Leone and Guinea to SE Nigeria. In a few localities, e.g. the Taï forest, Côte d'Ivoire, it is only locally distributed but numerous.

HABITAT Secondary growth within high forest; also along margins of the forest zone, and in swamp and palm forests. The Olive Colobus prefers to move and seek refuge in dense growth below 10m but may ascend to 30m, or even the canopy, when feeding with other species.

FOOD About 70% young leaves, buds and flowers, and only 10% mature leaves. The quantities of fruits and seeds vary seasonally but there is a strong preference for unripe fruits. Food is taken into the mouth directly off the plant.

BEHAVIOUR Groups of 5–15 animals tend to contain one adult male with several females and their young. Larger groups (of up to 20 animals) may have more than one adult male and could be aggregates of smaller units. The Olive Colobus is almost exclusively arboreal and extremely shy. The main response to any disturbance is to move into dense foliage and freeze in a hunched or crouched position in which the khaki colouring renders it very difficult to see. This behaviour is slightly modified when it is moving in mixed groups with guenons or mangabeys; it may then move temporarily into more open parts of the forest.

Females have perineal swellings and appear not to breed seasonally. During the first month after birth the very small young are carried in the mouth while the mother is moving. Later the infant may wrap itself around her neck or cling to her body.

The Olive Colobus communicates only infrequently, with very quiet chirping or burring calls.

ADAPTATIONS This species appears to be close to the lower size limit for a folivore.

STATUS The Olive Colobus has never been successfully raised in zoos and captive breeding is not an option. It is declining due to loss of forest habitats and hunting. Listed as Class A (African Convention), Appendix II (CITES), endangered (IUCN).

RED COLOBUS MONKEYS *Piliocolobus*

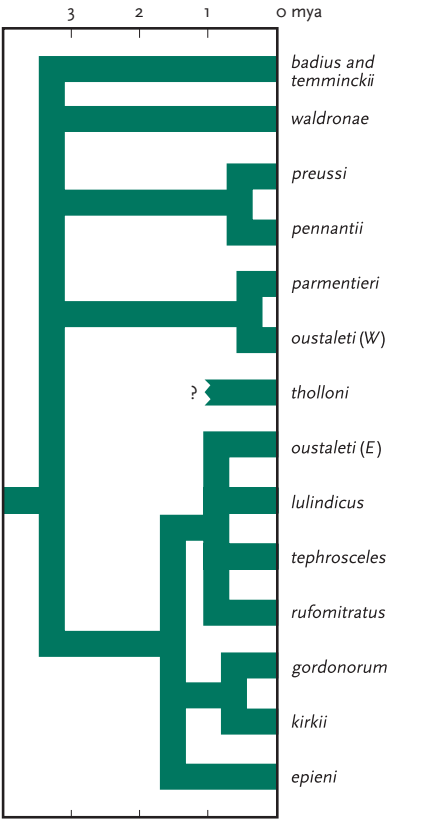
Zanzibar Red Colobus	*Piliocolobus kirkii*
Udzungwa Red Colobus	*Piliocolobus gordonorum*
Tana River Red Colobus	*Piliocolobus rufomitratus*
Tshuapa Red Colobus	*Piliocolobus tholloni*
Central African Red Colobus	*Piliocolobus oustaleti*
Niger Delta Red Colobus	*Piliocolobus epieni*
Pennant's Red Colobus	*Piliocolobus pennantii*
Preuss's Red Colobus	*Piliocolobus preussi*
Waldron's Red Colobus	*Piliocolobus waldronae*
Western Red Colobus	*Piliocolobus badius*

Note: The names given above try to reflect a diversity of discrete and widely scattered populations. All are provisional and several of the forms are sometimes united in *P. rufomitratus* as Eastern Red Colobus.

OTHER NAMES Fr. *Colobe bai.* Ger. *Roter Stummelaffe.*

MEASUREMENTS HB 410–700mm. T 420–800mm. W 5–13kg.

RECOGNITION Red colobus monkeys occur in numerous populations and species, some of which show much variation at the individual level while others are more uniform. All tend to be some permutation of red, white, black, brown and grey but build is the surest guide to recognition. They have exceptionally small heads on long-backed, pot-bellied bodies. The limbs are very long, with the legs slightly exceeding the arms in length. While the thumb is atrophied to a mere bump, the other fingers are aligned in a long, very powerful hook. All species tend to have dark or black faces, and some have pink lips, nose and eyelids. Young males have peri-anal swellings that appear to mimic the genital swellings of females.



Tentative phylogenetic tree for extant red colobus *Procolobus* (partly after Ting *et al.*).

Some taxa of red colobus: (a) Western Red Colobus *Piliocolobus badius*. (b) Niger Delta Red Colobus *Piliocolobus epieni*. (c) Tana River Red Colobus *Piliocolobus rufomitratus*. (d) Preuss's Red Colobus *Piliocolobus preussi*. (e) Central African Red Colobus *Piliocolobus oustaleti tephrosceles*. (f) Udzungwa Red Colobus *Piliocolobus gordonorum*. (g) Tshuapa Red Colobus *Piliocolobus tholloni*. (h) Montane race of Central African Red Colobus *Piliocolobus oustaleti foai*. (i) Zanzibar Red Colobus *Piliocolobus kirkii*.

DISTRIBUTION Equatorial forests from the Atlantic to the Indian Ocean but populations are extremely localised and always found near permanent water. In E DR Congo they occur up to 1,500m.
HABITAT Only in moist, evergreen forest close to permanent water. Although most red colobus monkeys are found in lowland forest, some occur in montane areas up to 1,500m. Possibly their distribution might have been determined by past climatic events and human hunting habits (both past and present) rather than by current vegetation patterns.
FOOD Red colobus monkeys are very selective of the plant types and parts that form the principal components of their diet but they eat many species in a single day. The proportions of fruits, seeds and young or old leaves are strongly influenced by local availability and by the feeding habits of other primates. Groups scatter to feed and can have a massive impact on the foliage of their food trees.
BEHAVIOUR Although small family groups are occasionally seen, they typically form large troops, numbering up to 100 animals. These form a territorial unit that remains strictly resident within a 25–150ha territory. Densities can approach 300 per km^2. The territory is vigorously defended against intruders and advertised by all group members calling with a variety of barks and chirps. The composition of territorial units includes many males that remain in the territory throughout their lives, but females may move between groups. Feeding is concentrated in two main sessions during

the morning and evening, with a period of inactivity during the middle of the day. Red colobus monkeys follow routines of movement and have preferred sites for sunbathing or sleeping.

Movement through the canopy is very characteristic, with animals crossing relatively wide gaps by leaping and catching slender supports with hooked hands or by setting up a catapult effect by rocking back and forth on a vertical stem. Some populations are more exclusively arboreal than others. Although some populations may be relatively shy, nearly all red colobus species are extremely vulnerable to hunting as they are noisy, conspicuous and relatively slow.

Young are carried, clinging to the belly of the mother for 3 months. Weaned at 1 year, females mature by 2 years of age and males at 3–3.5 years.

ADAPTATIONS Red colobus monkeys have a long digestive tract with a sacculated stomach that shows adaptations comparable with those of folivorous ungulates but is less specialised than those of pied colobus monkeys.

STATUS See individual entries below.

ZANZIBAR RED COLOBUS *Piliocolobus kirkii*

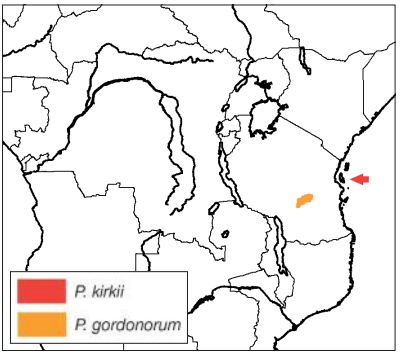
OTHER NAMES Kirk's Red Colobus. Fr. *Colobe de Zanzibar*. Ger. *Sansibar-Stummelaffe*.

MEASUREMENTS See under genus *Piliocolobus* (lower range of measurements).

RECOGNITION Colobus with a ragged, tesselated coat of three colours: red, black and white, individually very variable. The pink lips and nose form a strong contrast with the bare black skin on the rest of the face. The long, limp hair on the crown of the head is particularly characteristic. The vocalisations of this species are different from any other species.

HABITAT Occurring in relict patches throughout Zanzibar I., but found mainly in the southern part of the island and also in scrub forest growing on waterless coral rag on the eastern side. A small population has been translocated to Pemba I.

FOOD Some groups feed almost exclusively on mangrove leaves and the populations on coral rag appear to subsist on a drier, coarser diet than any recorded for red colobus monkeys. In the absence of any other colobus competitor, these populations show no disproportionate preference for leaf stems, but fruits and seeds comprise one-third of the diet while mature leaves are scarcely eaten at all. Young leaves, buds and flowers are the preferred parts. Bridelia, figs and Alexandrian laurel (*Calophyllum*) are the preferred species from a total of more than 60 food plants.



Zanzibar and Udzungwa Red Colobuses

STATUS In 1981 the total population was estimated at 1,500 animals distributed in 75 groups. Some groups show evidence of decline while others, notably those on Jozani, Muyuni and Uzi Is., appear to be healthy, stable groups. The Zanzibar Red Colobus is nominally protected and the formation of national parks on Zanzibar I. is currently under discussion. Listed as Class A (African Convention); Appendix I (CITES), endangered (IUCN).

UDZUNGWA RED COLOBUS *Piliocolobus gordonorum*

OTHER NAMES Iringa Red Colobus. Fr. *Colobe bai d'Udzungwa*. Ger. *Udzungwa Stummelaffe*.

MEASUREMENTS See under genus *Piliocolobus* (lower range of measurements).

RECOGNITION A polymorphic, often dark-toned species (red, brown, grey, black and white) with a thin, shaggy coat, less tesselated than the Zanzibar species and with two extreme types occurring, one dull with muted contrasts, the other more colourful and contrasty.

HABITAT Restricted to a few small forests on the Uzungwa Mts, where it survives in riverine and montane forest patches between 550 and 6,000m. The range is shared by Angola Colobus and other monkeys.
FOOD About two-thirds leaf stems (petioles) from some 35 tree species. Both ripe and unripe fruits make up nearly 20% of the diet, with buds, flowers, new leaves and very small quantities of older leaves making up the balance. Competition with other monkeys may explain why this species is a leaf-stem specialist. Selective clearance, reducing the colobus's food choice, will severely affect this species.
STATUS Recent systematic surveys and improved protection suggest a more positive situation than in the 1970s when this species suffered from the construction of a railway, combined with extensive logging and agricultural expansion. Although nominally protected by law, the animal is frequently hunted as a delicacy. Listed as Class A (African Convention), Appendix II (CITES), endangered (IUCN).

Udzungwa Red Colobus

Tana River Red Colobus

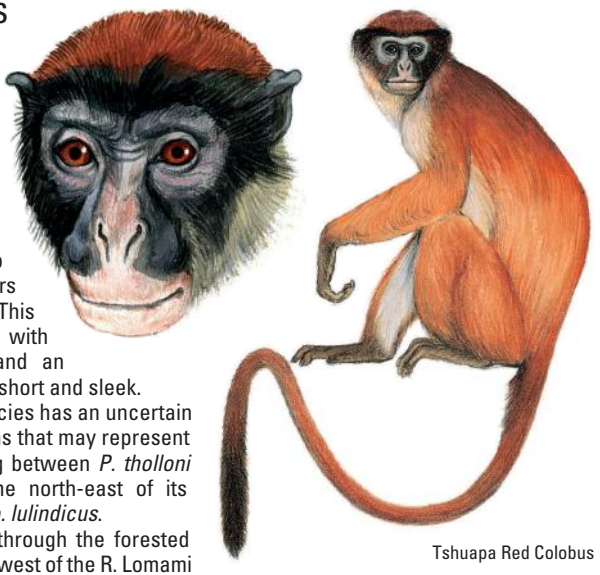
TANA RIVER RED COLOBUS *Piliocolobus rufomitratus*

OTHER NAMES Fr. *Colobe bai de la Tana*. Ger. *Tana Stummelaffe*.
MEASUREMENTS See under genus *Piliocolobus* (lower range of measurements).
RECOGNITION Colobus with a dull, greyish-brown back, paler greyish limbs and a grey-white underside. The russet cap with cow-licks above each ear is the only prominent feature. In spite of resembling some *P. oustaleti tephrosceles* in colour, it differs in size and skull shape.
HABITAT Frequenting riverine and gallery forest, only on the levees of the R. Tana between Kipendi village and the mouth of the river, notably the Mnazini and Kinyadu forests. These forests are dominated by *Pachystela* and *Barringtonia*.
FOOD On the R. Tana only 22 food trees are used by red colobus species, fewer than in any other area where this monkey has been studied. In spite of such a narrow choice, it maintains a similar range of food types to other populations. Diet comprises a quarter fruits and seeds, two-thirds buds, flowers and young leaves, and just over 10% of old mature leaves. This species is peculiarly dependent on the leaves and fruit of *Ficus sycomorus*.
STATUS Living in a dispersal group of 4–25, a 1972 census estimated a population of 1,860 individuals. By 1995 this had dropped to 1,200. This decline appears to have several causes: (a) drastic changes in vegetation due to dam construction and water diversion which changed the water-table; (b) forest clearance for agriculture; (c) fires eroding levee forests; (d) degradation due to livestock and wood collection; (e) selective felling of *Ficus* trees for canoes; (e) hunting. Nominally protected by law and listed as Class A (African Convention); Appendix I (CITES), endangered (IUCN). Now probably highly endangered.

TSHUAPA RED COLOBUS

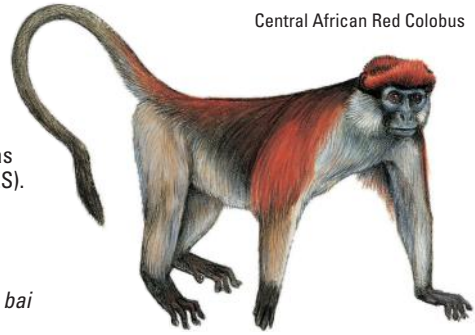
Piliocolobus tholloni

OTHER NAMES Fr. *Colobe bai de Thollon*. Ger. *Tshuapa Stummelaffe*.
MEASUREMENTS See under genus *Piliocolobus* (upper range of measurements).
RECOGNITION Of almost uniform foxy-red colouring, darkening to a deep brown on the shoulders and lighter on the underside. This colobus has a longer face, with a prominent square muzzle and an overshot lower jaw. The coat is short and sleek.
GEOGRAPHIC VARIATION This species has an uncertain relationship with two populations that may represent the product of long-term mixing between *P. tholloni* and colobus monkeys from the north-east of its range, *P. oustaleti langi* and *P. o. lulindicus*.
HABITAT Ranges intermittently through the forested areas south of the Congo R. and west of the R. Lomami in widely separated localities along rivers draining from the south into the Congo R.
FOOD Not yet studied.
STATUS Largely unknown but extensive expansion of human populations and cultivation from Kasai northwards and uncontrolled hunting are sure to have affected its status. Classified as insufficiently known (IUCN), it is listed with others of the Red Colobus group as Class B (African Convention), Appendix 2 (CITES).



Tshuapa Red Colobus

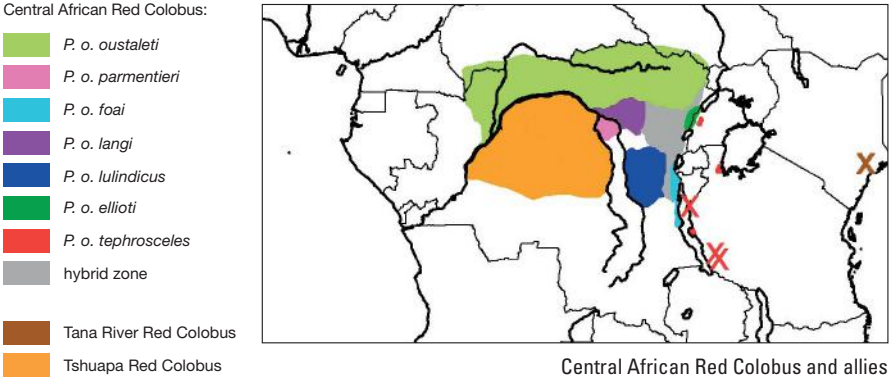
Central African Red Colobus



CENTRAL AFRICAN RED COLOBUS

Piliocolobus oustaleti

OTHER NAMES Eastern Red Colobus. Fr. *Colobe bai d'Ouganda*. Ger. *Uganda Stummelaffe*.
MEASUREMENTS See genus *Piliocolobus* (upper range of measurements).



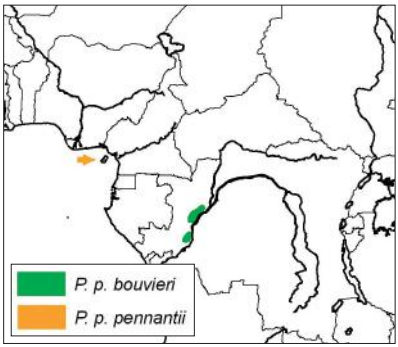
Central African Red Colobus and allies

RECOGNITION Some populations are relatively uniform and others are highly variable at the individual level. Most have dark extremities to the limbs (often black hands and feet), with red markings especially on the cap. Body sizes are among the largest of the red colobus radiation and montane populations tend to have thick coats, with the shoulder fur lengthened into a heavy cape in mature males.
GEOGRAPHIC VARIATION Twenty subspecies have been described of this highly variable species. Provisionally seven subspecies with definable ranges can be recognised (after M. Colyn): *P. o. oustaleti* (north of Congo R. and R. Aruwimi), *P. o. parmentieri* (R. Lualaba/R. Lomami junction); *P. o. foai* (Itombwe massif – very distinctive montane form), *P. o. langi* (between R. Aruwimi and R. Maiko – some *tholloni* traits), *P. o. lulindicus* between R. Lowa and R. Lualaba – some *tholloni* traits), *P. o. ellioti* (R. Semliki valley), *P. o. tephrosceles* (east of Rift Valley).
DISTRIBUTION Central Africa north and east of Congo R. to W Uganda and W Tanzania.
HABITAT Ranges between 300 and 2,500m, spanning a wide range of forest types from levee, swamp, lowland and mixed to montane forests.
FOOD The easternmost race, *P. o. tephrosceles*, has been studied in considerable detail. In Kibale (Uganda) young leaves and buds comprise nearly half and mature leaves a quarter of the annual diet. At Gombe, in Tanzania (a more markedly seasonal forest), these proportions are inverted. At both sites intense competition from frugivorous primates probably helps to explain their very minor consumption of fruits and seeds. Leaf stalks are also important at Kibale.
STATUS With a very wide scatter of populations, most in remote, seldom-visited areas, conservation status is insufficiently known. Some of the distinctive races or varieties included here are of very restricted distribution.

PENNANT'S RED COLOBUS

Piliocolobus pennantii

OTHER NAMES Bioko Red Colobus. Fr. *Colobe bai de pennant*. Ger. *Bioko Stummelaffe*.
MEASUREMENTS See under genus *Piliocolobus*.
RECOGNITION Boldly coloured monkey with black back, temples, hands, feet and tail. The flanks, forearm, thigh rears and tail-tip are bright red. Underside and chest cream, and limb innersides off-white. The crown is grizzled grey. A stark white ruff contrasts strongly with black temples and dark face. A radial parting of hair on the forehead is distinctive. Overall tints are paler in the mainland form.
GEOGRAPHIC VARIATION *P. p. pennantii* (Bioko I.), *P. p. bouvieri* (R. Lefini).



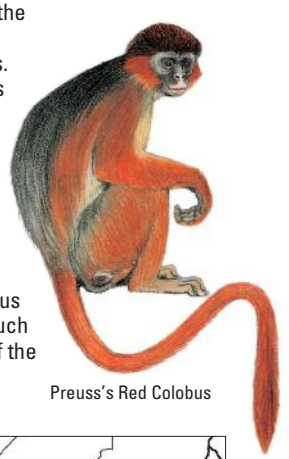
Pennant's Red Colobus

HABITAT This species poses a major biogeographical puzzle. Apart from the vestigial populations in Bioko I. and R. Lefini there are virtually no red colobus monkeys over most of central W Africa, which is otherwise a region of exceptional floristic and faunal richness. This near-elimination does not seem to be recent. Climatic changes, competition with other primates and past hunting by humans are all possible, but less likely, explanations than some major species-specific disease pandemic. The effects of such a catastrophe could have been long-lasting because all red colobus monkeys are poor dispersers. Neither the habitat nor the availability of food offers any clue to the relict status of these populations.
FOOD Not yet studied.
STATUS Nominally protected but intensively hunted throughout its range; critically endangered (IUCN).

Niger Delta Red Colobus

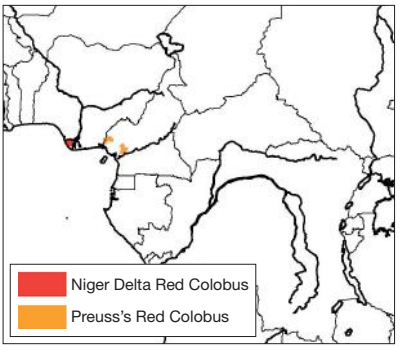
NIGER DELTA RED COLOBUS *Piliocolobus epieni*

OTHER NAMES Fr. *Colobe bai Nigerien*. Ger. *Niger Stummelaffe*.
MEASUREMENTS See under genus *Piliocolobus*.
RECOGNITION Mainly black and grizzled grey above with outer surfaces of hindlegs, lower flanks and elbows red. Hands and feet black. Undersides, chest and cheek margins creamy or off-white. Brow and central cheeks black. Tail reddish brown with black tip.
HABITAT This form, first noted in 1995, was subsequently allocated to *P. pennantii*, its nearest Red Colobus neighbour. However, a recent genetic study showed that its closest affinities are with red colobus species well over 1,000km to the east and not with *P. pennantii*. This has compounded the difficulties in interpreting the biogeography of red colobus monkeys.
FOOD Not yet studied but likely to be similar to other red colobuses.
STATUS Only known from a small sector of the Niger Delta, this species has been listed as one of the world's 25 most threatened primates. Its survival is already uncertain.


Preuss's Red Colobus

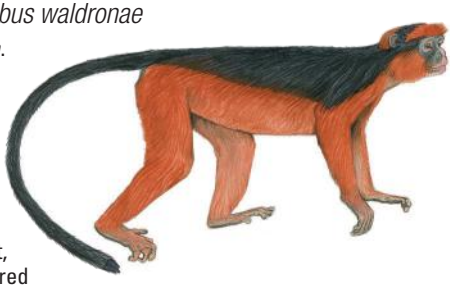
PREUSS'S RED COLOBUS *Piliocolobus preussi*

OTHER NAMES Fr. *Colobe bai de Preuss*. Ger. *Preuss Stummelaffe*.
MEASUREMENTS See under genus *Piliocolobus*.
RECOGNITION Tentatively treated as a distinct species this colobus shares some features (colour) with *P. pennantii* while others (such as hair-growth patterns on the head and nose shape) are typical of the western *P. badius* group.
HABITAT A vestigial population now restricted to an interface between the low-lying Cross R. and the formerly forested uplands of Cameroon.
FOOD Not yet studied.
STATUS Now restricted to forests within a strip 120 × 60km. Virtually no efforts are being made to curb an out-of-control bushmeat trade that is consuming this species among others. If some survive, their best chances are in the Korup NP and, perhaps, the Ejagham Forest Reserve. Listed as critically endangered (IUCN).



Niger Delta and Preuss's Red Colobuses

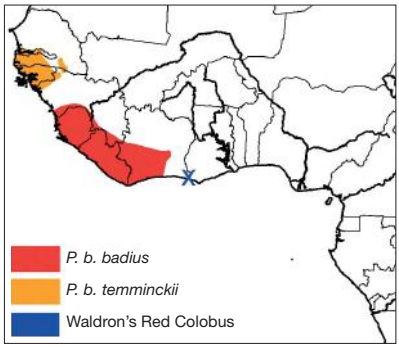
WALDRON'S RED COLOBUS *Piliocolobus waldronae*



OTHER NAMES Fr. *Colobe bai de M'me Waldron*. Ger. *Waldron-Stummelaffe*.
MEASUREMENTS HB 470–630mm. T 520–750mm. W 5.5–10kg.
RECOGNITION Formerly common in Ghana and Côte d'Ivoire east of R. Bandama, but now probably extinct from over-hunting. Genetic profiling has confirmed that this form merits species status. Distinguished by its flat, not-raised nose margins, all-black tail, rich red brow and forehead and red-tufted ears, red outer thighs, males with white scrotum.
HABITAT Rain forest and cultivation mosaics in area of high rainfall.
FOOD Diet likely to have been fruits and seeds, young leaves, buds and flowers.
STATUS Thought extinct; if so, represents the first permitted extinction of a distinctive primate in spite of authoritative warnings.

WESTERN RED COLOBUS

Piliocolobus badius

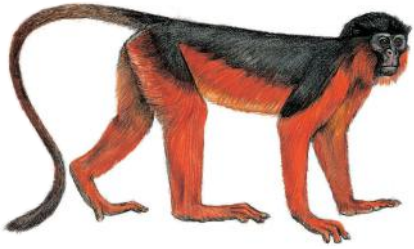


Waldron's and Western Red Colobuses

OTHER NAMES Fr. *Colobe bai d'Afrique Occidentale*. Ger. *Westafrikanischer Stummelaffe*.
MEASUREMENTS HB 470–630mm. T 630–800mm. W 5.5–10kg.
RECOGNITION Black or dark grey upperparts with lower limbs and underparts ranging from rich red to light orange. The face is characterised by a very flat profile but with the nostrils forming a peculiar swollen structure arising from a saucer-like depression.
GEOGRAPHIC VARIATION *P. b. badius* (Sierra Leone, Liberia, Guinea, Côte d'Ivoire), *P. b. temminckii* (Senegambia, Guinea Bissau, NW Guinea).
HABITAT Various forest types, including mangrove swamps, woodland and cultivation mosaics, especially in the north-western part of the range.
FOOD In Senegal, where there are fewer primates, less competition may explain why over a third of the diet is fruits and seeds (another peculiarity here is occasional consumption of bark). Young leaves, buds and flowers are the main food while mature leaves are very rarely eaten. Only 40 food plants have been recorded in Senegal. In Sierra Leone fewer fruits and seeds and more old leaves are eaten, reflecting the much higher levels of competition from other monkeys.
STATUS The range of this species is declining rapidly due to logging and increasing cultivation but it is nominally protected in several national parks or protected areas. IUCN lists as endangered.

P. b. temminckii
adult female

P. b. badius
adult male



PIED (BLACK-AND-WHITE) COLOBUS MONKEYS *Colobus*

Black Colobus	*Colobus satanus*
King Colobus	*Colobus polykomos*
Angola Colobus	*Colobus angolensis*
Geoffroy's Colobus	*Colobus vellerosus*
Guereza Colobus	*Colobus guereza* (syn. *C. abyssinicus*)

RECOGNITION Pied colobus monkeys are long-fingered, agile monkeys. Each species has a distinctively shaped face but they are best distinguished by their colouring. Except for the all-black *C. satanus*, all species sport patches of white fur that contrast strongly with the predominantly black body. These flashes appear on the chin, cheeks, shoulders, rump, thighs or tail. Their heavy bodies, long backs and limbs impart a bouncy gait that differs strikingly from the more fluent movements of guenon monkeys.

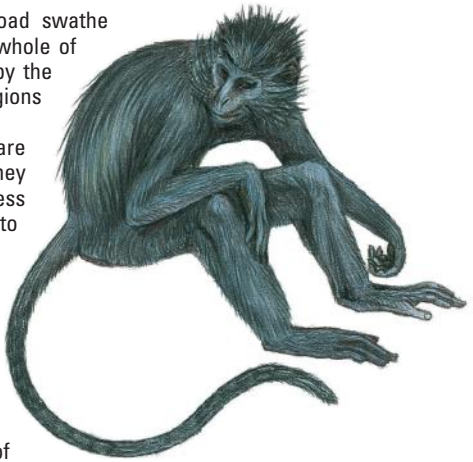
GENEALOGY Pied colobus radiation is exclusively African and predominantly tropical. In their ability to digest coarse, older material they are more specialised than the red colobus monkeys. This has allowed them to expand into drier, colder and more seasonal environments.

GEOGRAPHY Guereza Colobus, restricted to northern and eastern forests, appears to be the most cold-adapted form and may be the most recently evolved. They are likely to have colonised much of their eastern range during a cool dry period. North of the Congo R. overlaps in range between common Guerezas and the scarcer Angola Colobus might reflect the pre-eminence of Guerezas in recent cooler times superimposed upon the Angola Colobus, which represents older colobus stock.

ECOLOGY Pied colobus monkeys occupy a broad swathe of tropical and subtropical forests across the whole of Africa. Montane forests have been colonised by the Angola Colobus in more southerly and central regions and by Guerezas in the north-east.

NATURAL HISTORY Pied colobus territories are smaller than those of red colobus monkeys. They can subsist on material that is older and less palatable to the red colobuses. They also tend to feed from fewer tree species.

ADAPTATIONS The colouring of pied colobus monkeys is most conspicuous during daily chorusing around dawn and dusk, at which times animals climb into a prominent tree or onto the roof of the forest. Each group advertises its strength and numbers by joining together in very loud tattoos of croaking, with much jumping, branch-shaking and flouncing of tails and tassels, in a prolonged, ritualised threat display. The most extravagant movements, loudest calls and most aggressive postures are exhibited by dominant males.



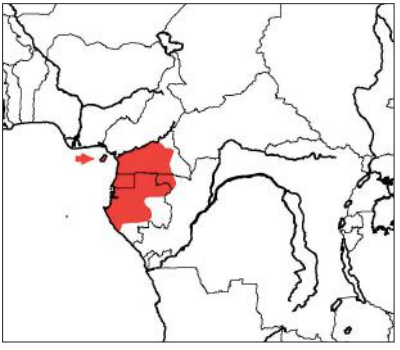
BLACK COLOBUS *Colobus satanus*

OTHER NAMES Satanic Colobus. Fr. *Colobe noir*. Ger. *Schwartzer Stummelaffe*.

MEASUREMENTS HB 500–710mm. W 6.6–13.2kg.

RECOGNITION All-black, without tassels or a tufted tail, and most like the Angola Colobus in general morphology but with straggly pelage. Has a shorter nose, thicker incisors and lacks the loud, reverberating calls of other species.

HABITAT Limited to high-canopy forests between



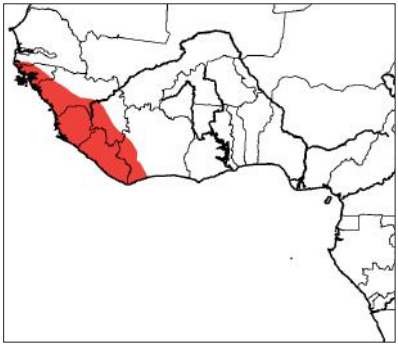
Black Colobus

SW Cameroon, Bioko I. and the Congo R. where it exists at about one-tenth the density of Pied Colobus in Uganda. Part of its mainland range is coastal sand-dune forests with an impoverished flora. Many of the local tree species, especially legumes, are protected by distasteful, or even toxic, compounds.

FOOD High proportion of seeds and unripe fruits. Shows a marked preference for leaves of lianas. In sand-dune forest young and old leaves are eaten equally. In the Ogooué basin scarcely eats old leaves at all but takes a larger proportion of fruits and seeds.

STATUS Low density and poorer diet might have reduced the value of energetic territorial behaviour. This could help explain why this species is duller in colouring and has a quieter vocal repertoire. Widely hunted, it is a popular and vulnerable quarry for hunters armed with shotguns or bows and arrows. It appears to be a weak colonist of secondary growth after logging and is currently declining in numbers in most parts of its range. Listed as Class B (African Convention), Appendix II (CITES), endangered (IUCN).

KING COLOBUS *Colobus polykomos*



King Colobus

OTHER NAMES Western Pied Colobus. Fr. *Colobe blanc et noir d'Afrique Occidentale*. Ger. *Weissbart Stummelaffe*.

MEASUREMENTS HB 500–610mm (♀), 500–670mm (♂). T 630–900mm. W 6.6–10kg (♀), 8.0–11.7kg (♂).

RECOGNITION Long-limbed and long-fingered, with intensely black body and legs, wholly white tail. Bonnet of straggly silver hair around face and long white epaulettes. Callosities fringed with narrow margins of white hairs.

GEOGRAPHIC VARIATION *C. p. polykomos* (west of R. Sassandra to Sierra Leone and S Guinea); *'C. p. dollmani'* (from east of the R. Sassandra) probably a hybrid with *C. vellerosus* in this very narrow contact zone.

HABITAT Rainforest and forest galleries are preferred.

FOOD Selective feeding habits; about one-third of total diet from 20 species of trees and lianas. Fruits and seeds more than a third of diet; buds, flowers and other foliage another third; mature foliage makes up the balance. Unripe seeds eaten but diet varies both regionally and seasonally. Strong preference for lianas, leguminous trees and *Strychnos* leaves.

STATUS Once common and widespread, habitat loss and hunting are responsible for a decreasing scatter of vestigial populations. Currently listed as vulnerable (IUCN.)

ANGOLA COLOBUS *Colobus angolensis*

OTHER NAMES Angola Pied Colobus. Fr. *Colobe d'Angola*. Ger. *Angola Stummelaffe*. Swah. *Mbega*.

MEASUREMENTS HB 480–660mm (♀), 520–740mm (♂). T 560–900mm. W 5.0–8.5kg (♀), 6.0–11.5kg (♂).

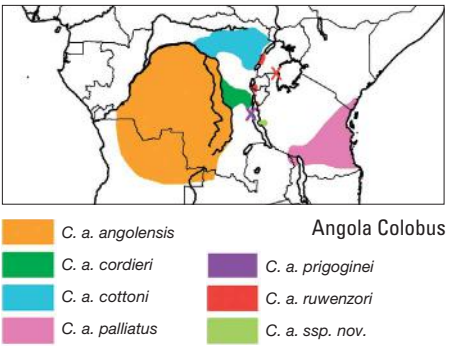
RECOGNITION Black-bodied colobus monkey with white ruff and long white epaulettes. Tail varies from all-white to nearly all-black. Coat short and thin in lowland forms but long and coarse in highland populations.

GEOGRAPHIC VARIATION *C. a. angolensis* (Congo R. basin south of river), *C. a. cordieri* (E DR Congo), *C. a. cottoni* (NE Congo R. basin, north of river), *C. a. palliatus* (Eastern Arc forests and Kenya/

Tanzania coastal forests), *C. a. prigoginei* (Mt Kabobo, DR Congo), *C. a. ruwenzori* (Rwenzori to Burundi). Further subdivision is possible (see illustrations below).

HABITAT Montane and lowland forests. In E Tanzania, Angola Colobuses are most concentrated at elevations between 400 and 1,000m.

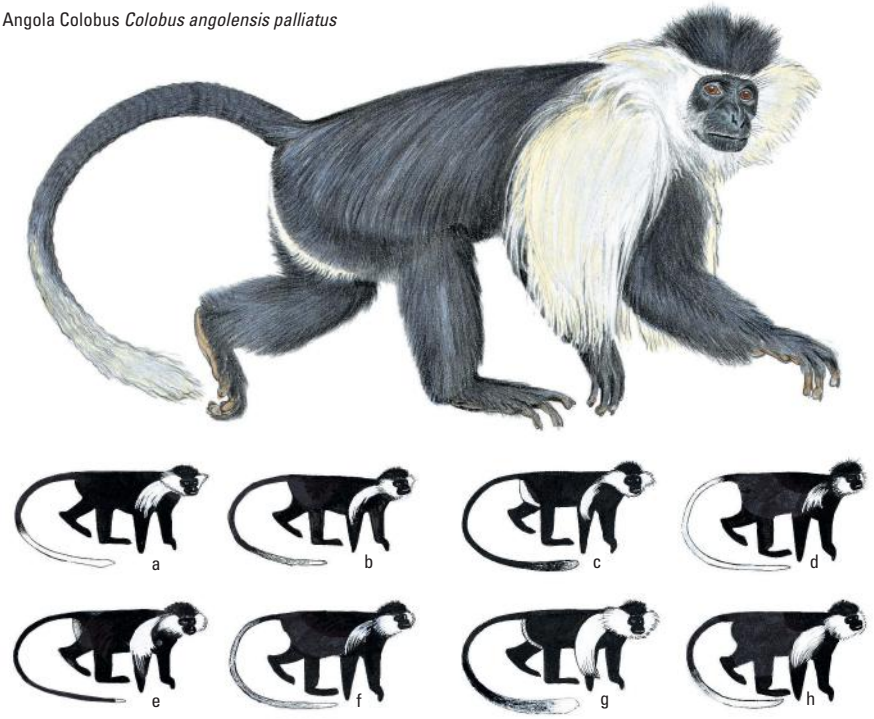
FOOD Diet like *C. polykomos* in combining about two-thirds of leaves with one-third fruits and seeds. In E Tanzania eats mainly ripe fruits and nearly a third of diet is mature leaf growth. Ability to subsist on old leaves could explain why the Angola Colobus has the most extensive range of any pied colobus monkey. Significantly they are either outnumbered or encircled by Guerezas on the margins of their range in parts of central Africa. This could imply that their original range in E Africa might have been eroded by the Guereza Colobus because of the latter's superior ability to digest cellulose and mature leaves.



Angola Colobus

STATUS As a species the Angola Colobus is of less concern but isolated populations on the E African coast and highlands are locally vulnerable or endangered.

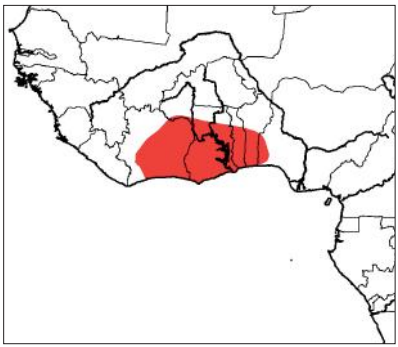
Angola Colobus *Colobus angolensis palliatus*



Colour/regional morphs of Angola Colobus: (a) *angolensis* (S Zaire basin). (b) *cottoni* (NE Zaire). (c) *'adolphi frederici'* (Kagera valley). (d) *prigoginei* (Mt Kabobo). (e) *ruwenzori* (central highlands). (f) *cordieri* (Uzimba). (g) *'sharpei'* (southern highlands). (h) *palliatus* (Eastern Arc forests).

GEOFFROY'S COLOBUS

Colobus vellerosus



Geoffroy's Colobus

OTHER NAMES White-thighed Colobus. Fr. *Colobe de Geoffroy*. Ger. *Geoffroy Stummelaffe*.
MEASUREMENTS HB 600–670mm (♀ and ♂). T 730–930mm. W 6.9kg (♀), 8.5kg (♂).
RECOGNITION Black-bodied monkey with broad white ruff encircling black face. White patch on thigh; white tail. Vestigial epaulettes of sparse white hairs. Facial profile and skull more like *C. guereza* than *C. polykomos*.
HABITAT Ranges between the R. Bandama to Benin and Togo in lowland rainforest and gallery forests. Voice and social structure resemble those of *C. guereza*, with only one male in smaller groups and only a few mature males in larger groups (up to 50 animals).
FOOD Tends to feed in more shaded, middle layers of the forest when mixed with red colobus monkeys (which prefer rapid regrowth canopy foliage near the forest roof). Diet is thought to resemble that of *C. guereza*, but exact composition may vary according to presence or absence of other monkeys.
STATUS Currently listed as vulnerable (IUCN) but likely to become endangered if present rates of habitat change and hunting continues.

Geoffroy's Colobus

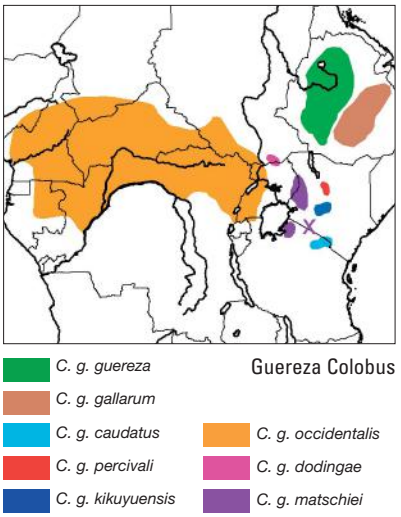
GUEREZA COLOBUS *Colobus guereza* (syn. *C. abyssinicus*)

OTHER NAMES Fr. *Colobe guereza*. Ger. *Guereza Mantelaffe*. Swah. *Mbega*.
MEASUREMENTS HB 480–670mm (♀), 535–700mm (♂). T 520–900mm. W 5.4–10.9kg (♀), 6.4–14.4kg (♂).
RECOGNITION Black-and-white monkey with shorter, thinner fur in lowland forests but very long and thicker fur in mountain areas. White on tail and mantle most extensive in easternmost populations. In west, black shoulders and tail root more extensive.
GEOGRAPHIC VARIATION *C. g. guereza* (includes *gallarum*) (Ethiopia), *C. g. caudatus* (includes *percivali*, *kikuyuensis*) (E African mountains), *C. g. occidentalis* (includes *dodingae*, *matschiei*) (E Nigeria to W Kenya).

Guereza Colobus, highland East African form, *C. g. caudatus*

HABITAT Wide-ranging, from lowland tropical rainforest to upper reaches of montane forest, as well as riverine galleries and evergreen thicket forests. Where range of Guerezas overlaps with red colobus monkeys, they usually feed from less than half the number of species and choose different plant parts. A less varied diet allows them to occupy forests or thickets with impoverished or specialised floras. They can survive in drier, more degraded forests.

FOOD In all areas where they have been studied, Guerezas have been found to be the most folivorous colobine species except for the Olive Colobus, which takes almost identical ratios of plant parts (lack of any overlap suggests they may be competitively exclusive). About three-quarters or more of diet consists of leaves but proportion of old leaves varies with locality and season, influenced by the presence/absence of other monkeys. For example, where Guerezas and red colobuses feed on *Markhamia*, the former eat leaf-blades and the latter strip out and consume petioles alone.



BEHAVIOUR Guerezas live in small territories where several related offspring live with one or more hierarchically ranked males. Mutual male intolerance forces males to disperse and promotes female cohesion.

STATUS Guerezas were once abundant in most parts of their lowland range but are declining in many localities. In Ethiopia continuous habitat loss and hunting over centuries has reduced a formerly very extensive range to a wide scatter of relict populations. Still abundant in E African forest reserves and parks but declining elsewhere. As Guerezas are not considered to be endangered, IUCN gives them a low conservation rating. However, unrestricted trade in their skins could lead to extinction of the eastern montane populations that have the most desirable pelts and the most restricted distribution.

Guereza Colobus, central African lowland form,
C. g. occidentalis

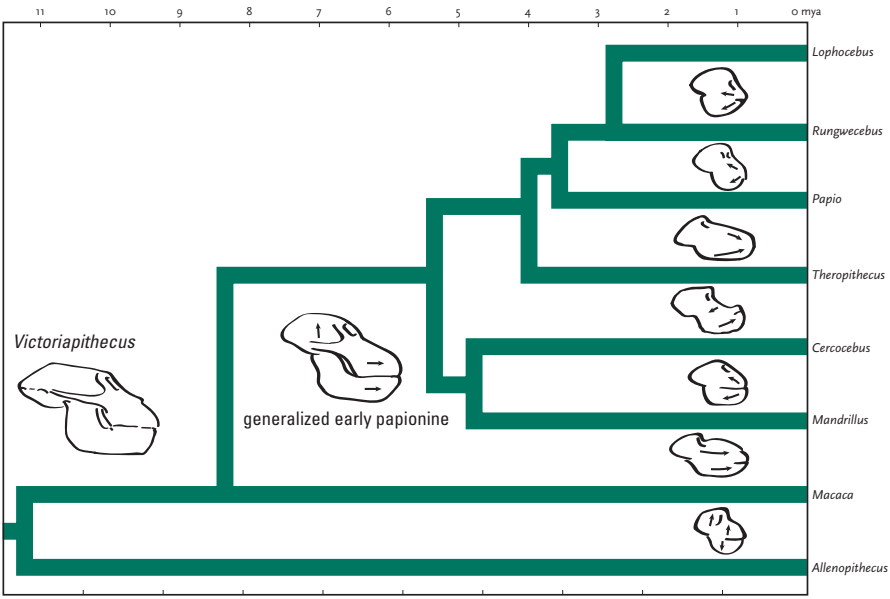
CHEEK-POUCHED MONKEYS CERCOPITHECINAE

Baboons	*Papio* (5 species)
Kipunji	*Rungwecebus kipunji*
Baboon-mangabeys	*Lophocebus* (2 species)
Gelada	*Theropithecus gelada*
Mandrills	*Mandrillus* (2 species)
Drill-mangabeys	*Cercocebus* (7 species)
Barbary Macaque	*Macaca sylvanus*
Guenons and allies	*Cercopithecini*

RECOGNITION This subfamily embraces all the non-colobine African monkeys. They vary greatly in size, colour and shape, ranging from the miniature, round-headed talapoins to heavily built, long-faced baboons and drills. The more arboreal lowland species tend to have longer tails; terrestrial and montane species have shorter tails. As their popular name indicates, all these monkeys have voluminous sacs beneath each cheek.

GENEALOGY This family is thought to derive from the main-line branch of 'Victoria monkeys', which continued as omnivores in (probably southern) drier habitats after separation from early colobines (probably in more equatorial regions). There are two main subfamilies of cheek-pouched monkeys: 'baboon-macaques', or Papionini; and guenons, or Cercopithecini. Once proto-baboons and proto-macaques had differentiated, the latter spread into Eurasia (where they speciated into many forms) while the baboon group radiation continued within Africa.

Among the earliest 'baboons' were at least seven species of grass-eating geladas (including a gorilla-sized one). They flourished from one end of the continent to the other but are now reduced to relict populations of a single species in the Ethiopian mountains. True baboons also radiated into numerous forms and one branch, the drills, colonised the equatorial forests of central-west Africa. These early drills and baboons probably gave rise to smaller more arboreal forms that survive as 'mangabeys' and the Kipunji. In spite of their resemblances, molecular evidence suggests that Kipunjis, 'baboon-mangabeys' and 'drill-mangabeys' are parallel derivatives from two,



Tentative phylogenetic tree for Papionini (partly after Tosi *et al.* 2005). Arrows suggest directions of cranial extension or contraction.

perhaps three, more terrestrial ancestors. The failure of baboons to get beyond Africa, and the success of early macaques in crossing extensive arid barriers, is explained by the latter's ability to tolerate extremes of temperature and live off the poorest, most difficult land. Well illustrated by several living macaque species, this is no recent development because fossils show that Barbary Macaques have lived along the edges of the Sahara for more than 6 million years.

Tolerance for extremes of temperature, relatively small size, cheek pouches and sophisticated social systems allow macaques to exploit mangrove swamps, seashores, floodplains and other habitats with harsh seasonal or daily changes. That early macaques succeeded in colonising these difficult environments is suggested by the existence of Allen's Swamp Monkey, which is as much a relict tropical African macaque as it is a guenon.

Talapoin monkeys appear to be the culmination of a trend toward miniaturisation in an early stock of 'tropical macaques'. Talapoins and Allen's Swamp Monkey retain such macaque-like characteristics as sexual swellings of the females but also point to the emergence of the guenon group, Cercopithecini. The guenon radiation is outlined later (see p.139).

GEOGRAPHY Living cheek-pouched monkeys inhabit many geographical and climatic extremes. The Barbary Macaque inhabits the N African littoral and mountains. Baboons range through many habitats, both dry and humid, from the Cape of Good Hope to Cape Verde. Within equatorial Africa both subfamilies are represented from the two extremes of climate. Desert baboons and the Sahelian patas inhabit dry environments whereas drills and most guenon species live in moist forests.

ECOLOGY Almost all species are dependent on water or relatively moist foods but cheek-pouched monkeys remain the most arid-adapted of all primates. Secondary re-invasion of moist habitats is thought to be most recent in the guenons, less recent for the mangabeys and earliest in the case of the drills.

NATURAL HISTORY African cheek-pouched monkeys are the epitome of agility, speed and ingenuity. Bright colours, ritualised swaggering, head-bobbing and emphatic facial expressions serve highly specific and elaborate systems of visual communication. Mixed groups of monkeys are common, especially among the smaller, most arboreal species, a strategy that helps increase vigilance against predators as well as reveal more food.

As the most numerous and widespread primates in Africa, cheek-pouched monkeys represent a major disease reservoir and the natural history of monkey diseases has special importance for Yellow Fever epidemiology and for understanding the nature of human AIDS. Many African monkeys are resistant to AIDS. The monkey retrovirus, SIV, is genetically closer to human HIV2 than either of them are to the main human aids virus, HIV1. In the course of understanding how and why wild African monkeys are naturally resistant to AIDS, better ways of protecting humans are being developed.

ADAPTATIONS The diagnostic cheek pouches of these monkeys clearly evolved after their ancestors split away from the colobines, which lack them. The most likely context for their evolution would have been competitive feeding on sparse foods in dangerous, exposed environments. This is evidently an effective strategy for the semi-terrestrial, open-country species, but tree-dwelling in closed forests is a more recent adaptation.

BABOONS *Papio*

Sacred Baboon	*Papio hamadryas*
Guinea Baboon	*Papio papio*
Olive Baboon	*Papio anubis*
Yellow Baboon	*Papio cynocephalus*
Chacma Baboon	*Papio ursinus*

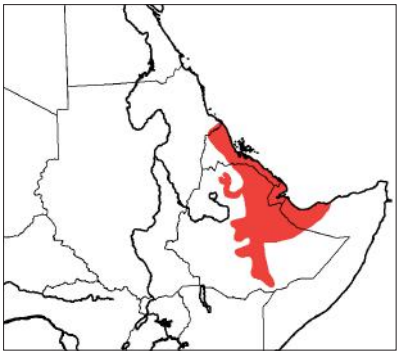
RECOGNITION Baboons are predominantly quadrupedal, brownish, grizzled terrestrial monkeys among which adult males are both bigger and longer-muzzled than females. The similarity of females from all regions has encouraged the view that male differences are merely subspecific. However, there are many anatomical and behavioural differences that distinguish five major populations, treated as species here.

GENEALOGY Fossil baboons from S and E Africa go back at least 3 million years. Following an initial dispersal over all sub-Sahara savannas, northern and southern populations emerged. The smaller Guinea and Sacred (Hamadryas) Baboons (which have several features in common) are northern derivatives. The other, bigger baboons derive from a single southern group. These originally southern baboons bisected the former northern population and expanded both eastwards and westwards. Guinea Baboons appear to be the westernmost relict of this retreat (but electrophoretic studies suggest that Olive Baboons have assimilated Guinea Baboon genes along the way). The East African Yellow Baboon also seems to have bisected a formally continuous range by interposing itself between the Olive and Chacma Baboons (another closely related pair).
ECOLOGY The ecological implications of this interpretation are that Yellow Baboons have become particularly well adapted to fire-climax woodlands. Their expansion westwards could be very recent if this type of vegetation has spread through human use of fire. If the northern baboons were originally adapted to drier and colder conditions than the southerners, it is possible that Olive Baboons owe their present vast range to quite recent changes in climate. It is known that the last and penultimate Ice Ages were followed by warmer, wetter weather and more wooded environments. This would have suited Olive Baboons better than either Guinea or Sacred Baboons. Present distributions are best explained by some such sequence of events but the timing remains highly speculative.
NATURAL HISTORY Both Guinea and Sacred Baboons live in minimal social units consisting of a male and up to five females with their offspring. These harems allow the animals to be more dispersed than is the case with the large multi-male groups typical of other species. Large groups are more destructive but the impact is offset in richer habitats.
ADAPTATIONS The heavy canine teeth of baboon males and their entire tooth-row are cantilevered out from the skull as far as is mechanically feasible. This extreme projection of the muzzle allows male baboons to make visually emphatic signals, such as ritualised yawns (as well as providing very long, seed-grinding molar surfaces). This kind of signalling is especially important for regulating male relationships. The male's muzzle is enhanced by a bare face surrounded by a big, circular ruff or cape of hair. Social display of these features, punctuated with loud, explosive barks, deters both potential rivals and predators.

Gross sexual dimorphism in these large, open-country monkeys allows males to be scouts and protectors for the group as a whole. It is also a factor that enables the principle of 'armoured truce' to bring order to aggregations at sleeping, feeding or drinking sites.

SACRED BABOON *Papio hamadryas*

OTHER NAMES Hamadryas Baboon. Fr. *Hamadryas*. Ger. *Mantelpavian*, *Hamadrayas*.
MEASUREMENTS HB 500–650mm (♀), 700–950mm (♂). T 400–600mm. SH 400–500mm (♀), 500–650mm (♂). W 10–15kg (♀), 15–20kg (♂).
RECOGNITION A grizzled, greenish-brown monkey, except for sexually active harem males which are grizzled dove-grey, with lighter cheek ruffs, tail tip and callosity margins, and darker hands and



Sacred Baboon

feet. The face and callosities are flesh-coloured. Callosities are largest and brightest in dominant males and apparently mimic female sexual skin.

HABITAT Arid subdesert, steppe, hillsides, escarpments and mountains bordering the Red Sea. Ranges through E Ethiopia from Suakin (Sudan) to Somali border (also in SW Arabia). The basic social unit consists of a single male with one or more females (a harem), who are abducted while still immature or 'inherited' from an aged male. Males are coerced by harem masters who initiate all the group's movements. Harems whose members are related by blood frequently sleep together or gather when foods are concentrated. These associations, called 'clans', occasionally converge to form 'bands' on a single resource, especially sleeping-cliffs. Very occasionally several hundred animals may come together at common feeding or sleeping sites to form a regional 'troop'.

FOOD Opportunistic omnivore. Grass, buds, invertebrates and the fruits of desert plants, notably heglig (*Balanites*) and buffalo thorn (*Ziziphus*), are of great seasonal importance.

STATUS Agricultural expansion and irrigation projects lead to conflict. The fine, long-haired capes of adult males are used to embellish ceremonial cloaks in Ethiopia. Large numbers of these baboons were formerly trapped for medical research in the former USSR.

The former range of this baboon extended into Egypt where it was held sacred to the Ancient Egyptian god Thoth. Free-living baboons in the temple of Thoth were regarded as priests to the god of Learning and Lord of Time. They were also used by Ancient Egyptian 'police' to arrest malefactors.

Listed as vermin (African Convention), Appendix II (CITES).

GUINEA BABOON *Papio papio*

OTHER NAMES Fr. *Babouin de Guinée*. Ger. *Sphynx-pavian*.

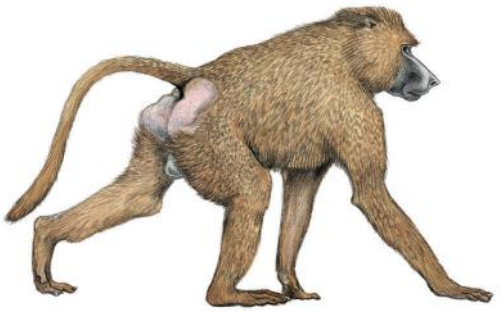
MEASUREMENTS HB 550mm (♀), 750mm (♂). T 350–600mm. SH 450mm (♀), 600mm (♂). W (est.) 12kg (♀), (est.) 19kg (♂).

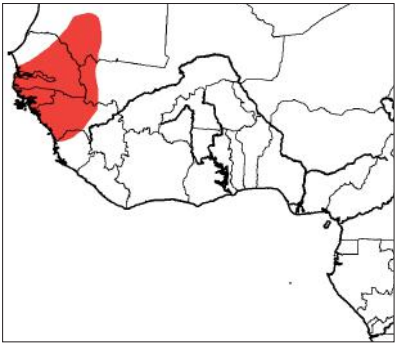
RECOGNITION A grizzled, reddish-brown baboon with a sharply defined cape on adult males. There are prominent nostrils above the mouth and dark pink skin on the face and callosities. The tail is smooth and 'unbroken'.

HABITAT Woodlands, savanna and Sahelian steppe within reach of water; gallery forests in south of range. Ranges from S Mauritania to Sierra Leone. Along its SE limits the Guinea Baboon seems to be hybridising with the larger Olive Baboon. Richer food resources and protection in Niokolo Koba NP, Senegal, allow large aggregations of harem groups, numbering 10–200 (sometimes exceeding 500) individuals, to forage together.

FOOD Seeds, shoots, roots, fruits, fungi, invertebrates, small vertebrates and eggs. Where agriculture has expanded, rice, maize, yams, groundnuts and other cultivated crops are also taken.

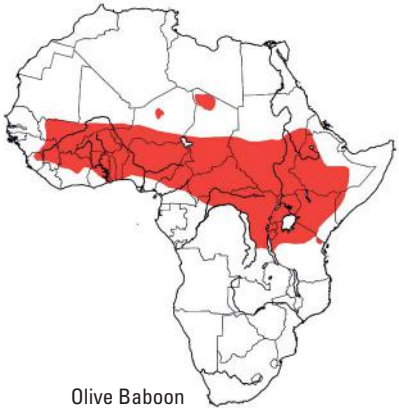
STATUS Protected in Niokolo Koba NP, where densities of 2–15 per km² have been estimated. Agricultural expansion, tree-felling and direct hunting for laboratory specimens or crop protection have caused widespread decline elsewhere. It is uncertain whether the Olive Baboon is currently expanding westwards. IUCN has recently revised the status to near threatened.





Guinea Baboon

OLIVE BABOON *Papio anubis*



Olive Baboon

OTHER NAMES Fr. *Babouin doguera*. Ger. *Anubis-pavian*. Swah. *Nyani*.

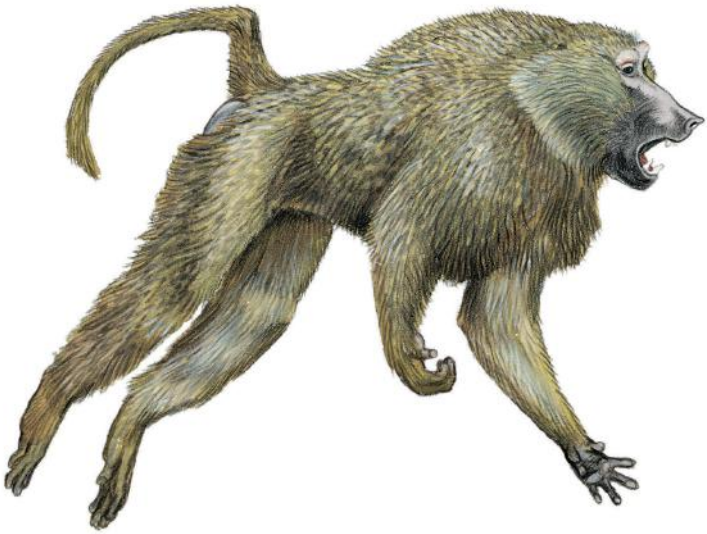
MEASUREMENTS HB 610–730mm (♀), 620–838mm (♂). T 310–600mm. W 6.3–18kg (♀), 7.9–29.5kg (♂).

RECOGNITION A large, grizzled, olive-brown or khaki monkey. Adult females have a thick cape over the neck and shoulders and shell-shaped greyish cheek ruffs. The face is naked and dark grey, with the nostrils projecting beyond the lips. Fused tail bones cause a sharp angle to form in the tail as if it were broken.

HABITAT The most extensively distributed of all baboons, ranging throughout Sahelian woodland and forest-mosaic habitats from S Mauritania and Mali to the Sudan and southwards to DR Congo and Tanzania. Outlying populations inhabit the Tibesti and Aïr massifs in the Sahara. In E Africa distribution is bounded by changes in vegetation rather than well-defined geographic barriers. Wherever the large Olive Baboon's range encounters that of other species there are hybrid zones and a strong implication that this species is still in a phase of active expansion.

FOOD Grass is a principal food in open areas, and fruits in forests. Resin or gum act as buffers in dry seasons and locusts provide the occasional glut. As an omnivorous opportunist the Olive Baboon changes its diet depending on the region, the season and even the time of day. Differences in social organisation and behaviour follow from its varied feeding strategies and habits. Males may form associations or 'cabals' that cooperate in some situations and develop a hierarchy in others. Male–female alliances can also form. Female hierarchies can escalate into family hierarchies; thus juveniles from high-ranking families can coerce or threaten older animals from lower-ranking ones. In competition over food, groups with more males prevail. This is the incentive for the large troops that form in all baboon species.

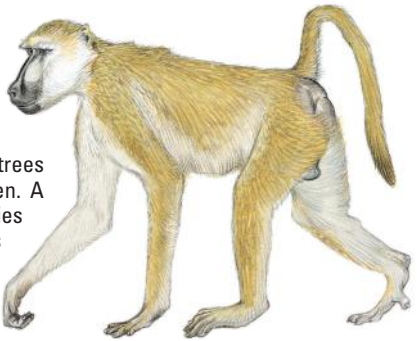
STATUS Overall distribution suggests it has caused the ranges of neighbouring, smaller baboons to contract. Probably excluded from closed forests by competition and disease. Remains widespread and common in spite of vigorous trapping, shooting and poisoning campaigns.



YELLOW BABOON *Papio cynocephalus*

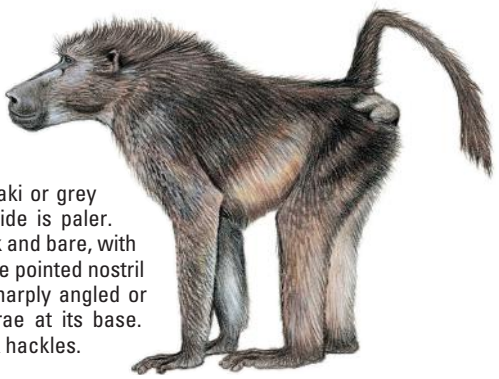
Yellow Baboon

OTHER NAMES Fr. *Babouin cynocéphale*. Ger. *Steppen-pavian*, *Barenpavian*. Swah. *Nyani*.
MEASUREMENTS HB 550–680mm (♀), 620–840mm (♂). T 380–560mm. W 9.1–16.8kg (♀), 18.6–30kg (♂).
RECOGNITION A slender baboon with brindled yellow-brown upperparts, tail and outer limb surfaces. Pale off-white below, it lacks cape or mane. There are prominent patches of white hair on the bare-skinned, dark grey muzzle and the nostrils are set back from lips.
GEOGRAPHIC VARIATION *P. c. kindae*. Baboons from west of L. Tanganyika and L. Malawi (L. Nyasa) and on both shorelines of L. Tanganyika are of smaller, paler 'Kinda' type.
HABITAT Ranges from Somalia to the Zambezi valley and across south-central Africa to Benguela (Angola). Over a great part of this area it is specific to fire-climax miombo (*Brachystegia*) woodland. Both within this zone and especially to the north-east the Yellow Baboon also occupies dry bushland, thickets, steppes and the coastal littoral (including mangroves). The predominantly leguminous trees produce abundant seeds, many of which are eaten. A preference for foods with an unusual chemistry implies that this baboon has acquired special adaptations in its digestion. This may help to explain why the boundaries of its distribution do not follow any geographic discontinuities but coincide very closely with the distribution of a plant community.



FOOD The seeds, flesh and pods of leguminous trees, such as *Acacia*, *Albizia*, mopane (*Colophospermum*) and Tamarind, are seasonal staples but miombo fauna, such as mopane worms and various other insects, are equally important at times. An opportunistic omnivore, like all baboons, it also eats grasses, shoots, fungi, lichens and many invertebrates. The Yellow Baboon typically forages in extended, well-spaced troops that can occasionally number up to 300 animals, with an average of between 30 and 80. During the calving season many young antelopes and hares are caught.
STATUS Commonly exported from E Africa for biomedical research, this species has been heavily trapped in several areas. It is still widespread and common, in spite of being locally displaced by agriculture and tree clearance in many areas.

CHACMA BABOON *Papio ursinus*

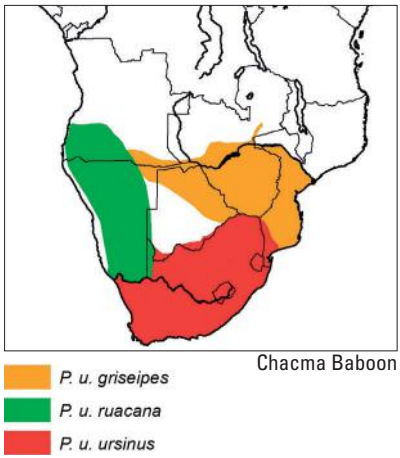


OTHER NAMES Fr. *Chacma*. Ger. *Tchakma*. Swah. *Nyani*.
MEASUREMENTS HB 550–680mm (♀), 670–755mm (♂). T 410–605mm. W 12–30kg (♀), 25–45kg (♂).
RECOGNITION Colour varies from grizzled khaki or grey to very dark brown and black. The underside is paler. Males have very long, narrow muzzles, black and bare, with paler patches between eyes and nostrils. The pointed nostril septum rises directly above the lips. The sharply angled or 'broken' tail is reinforced by fused vertebrae at its base. Adult males may have recurved hair on neck hackles.

GEOGRAPHIC VARIATION *P. u. griseipes* (between Zambezi and Limpopo rivers): paler ochre with grey extremities. *P. u. ruacana* (N of Orange R through Namibia to S Angola and W Kalahari): smaller, light-brown flanks and limbs, extremities brown to black. *P. u. ursinus* (S of Limpopo and Orange rivers): grey with black extremities. Clines between the three populations render animals from central areas of range indeterminate.

HABITAT Occupies all types of woodland, savanna, steppes and subdesert, montane, Cape and Karoo flora. Cliffs, kopjes or large trees are necessary night-time retreats. Water also limits its overall range in Namibia.

Densities can rise from three or four up to 43 per km² in protected localities. Troops range between 20 and 50 animals (up to 100). Multi-male hierarchies are normal.



Chacma Baboon

FOOD An opportunistic omnivore, showing local preferences for bulbs, roots, shoots, seeds or fruits. Invertebrates, small vertebrates, seashore life, fungi and lichen are eaten as and when available. Crops and young livestock taken in settled areas.

STATUS Common and widespread; totally dependent on drinking daily and artificial water supplies have allowed substantial expansion of territory.

KIPUNJI *Rungwecebus*

A newly named papionine genus from the southern highlands of Tanzania with physical, genetic and behavioural resemblances with both *Papio* and *Lophocebus*. It has been suggested that the Kipunji might represent a hybrid between an archaic *Papio* and an extinct *Lophocebus* species. On the basis of more recent genetic analyses the scientific discoverer and describer of this genus and species, Dr Tim Davenport, disagrees. Instead he has concluded that the new evidence supports *Rungwecebus* deriving directly from a *Papio*-like ancestor. This implies that a short-muzzled monkey can derive from a long-muzzled one; a controversial conclusion on which scientific opinion remains split because it had long been assumed that baboons derived from short-muzzled arboreal ancestors like mangabeys or, indeed, like the Kipunji.

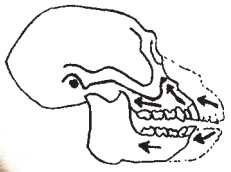
The issue is relevant not only for evolutionary anatomists and taxonomists but also for interpreting why *Rungwecebus* is now so precariously rare. Understanding the reasons for such rarity raise general issues about the conservation of montane biota as well as specifics in conserving the last of the Kipunjis. Furthermore, if *Rungwecebus* represents the relict of an early proto-*Lophocebus* stock, as now seems likely, the dynamics of evolutionary exchange between biota from the south–east and centre–west realms become more complicated as well as more comprehensible. The forest type to which Kipunjis are limited today are tiny vestiges of the forest cover typical of the Plio-Pleistocene glacial epochs. In the course of a long succession of glaciations after 2.7 mya a significant number of African flora and fauna succeeded in adapting to cold conditions on highlands, even on the Equator. The habits and habitat of *Rungwecebus* leave little doubt that these monkeys manifest just such an adaptive trend. Two-million-year-old fossils from Kenya are currently allocated to *Lophocebus* but probably sample highland monkeys that were closer to a *Rungwecebus* precursor than to equatorial lowland *Lophocebus*. Potential colonisers of high montane forests were more likely to be of southern, rather than of tropical, origin because already temperate-adapted monkeys had the best chance of adapting to steadily cooling conditions.

In spite of a putative baboon ancestor's physiological advantages, its adoption of a wholly arboreal existence would have demanded significant social and anatomical adjustments in a previously terrestrial or semi-terrestrial primate. The behavior and ecology of *Rungwecebus* would seem to accommodate just such a re-ordering of ecology, behaviour and morphology. For example, baboons range very widely. By contrast *Rungwecebus* have home-ranges of 1.6–4.3km². Baboon multi-male groups can number as many as 130 individuals: Kipunji groups number 15–39 and can

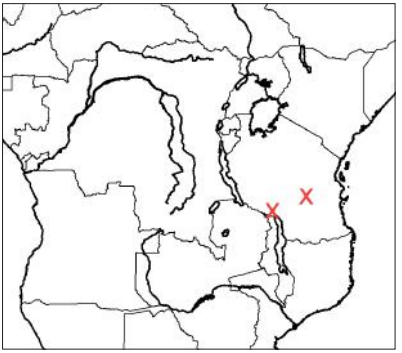
also include more than one male. Baboon males can weigh in at more than 30kg. The largest Kipunji males are estimated to weigh about half as much and sexual differences in size are much less apparent. As well as body-weights of the sexes being closer, Kipunji faces show much less sexual dimorphism than do those of baboons and the details of cranial anatomy reveal how this has been achieved. When a *Papio* skull is compared with that of a Kipunji (see figure below) it is clear that the latter's dental arcade is not only smaller in size but buckling of the jugal plate and zygomatic arch into an S-bend provides evidence for a phylogenetic backward shift of the entire muzzle. On living Kipunjis the external evidence for this wholesale retraction of their muzzles is manifested in conspicuous dimples under the eye sockets, a feature shared by all 'mangabey' species.

While the evidence strongly favours a close and, perhaps, direct relationship with *Papio* or the extinct *Parapapio*, affinities with *Lophocebus* suggest that the latter derived from the same montane ancestral lineage as *Rungwecebus*, but eventually acquired features that took it into lowland rainforests distancing it further from its *Rungwecebus*/*Papio* roots (as argued in the *Lophocebus* profile).

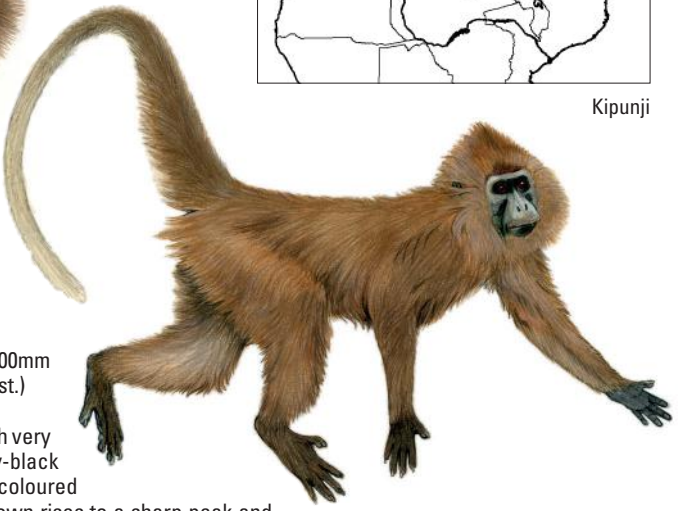
A concerted effort to study the biota of the Marungu/Malimba massif might throw some light on these questions.



Kipunji skull (juvenile). Arrows suggest evolutionary retraction from longer-muzzled ancestor.



Kipunji



KIPUNJI

Rungwecebus kipunji

MEASUREMENTS HB 850–900mm (♂, est.). W 10–16kg (♂, est.)

RECOGNITION A cinnamon brown, woolly monkey with very dark hands, feet and grey-black face and a pale cream-coloured tip to the long tail. The crown rises to a sharp peak and the ears are lost to view within a halo of long, dense fur.

For a baboon-like papionine the sexes are surprisingly similar in size and appearance. Kipunjis utter very baboon-like grunts and males make a deep honking bark (most often in the early morning and evening) which has been interpreted as serving to space out groups that have overlapping ranges but actively avoid direct contact. All sexes and ages make stereotyped head-shakes that are made more conspicuous by a pointed crest.

HABITAT An inhabitant of upper montane forests in the Southern Highlands of Tanzania. One reason for the late scientific discovery of this new genus and species (first described in 2005 and restricted to two forest areas) was that the principal part of their range was within a previously uncultivated,

steep and chilly zone first allocated to recent Safwa immigrant farmers by Nyakyusa authorities during the 20th century. Knowledge of these monkeys therefore remained restricted to an immigrant group of people whose existence was marginal and dialect outside the local mainstream.

FOOD 98% plant foods and 2% insects may reflect the scarcity of animal foods as well as a specific preference. Fruits, mainly eaten during the rains account for 27%, including the seeds and arils of wild poplar, *Macaranga capensis*. Leaves become most important during the dry season.

ADAPTATIONS The thick woolly coat of this species and its restriction to the cold upper regions of montane forests implies that this must be a relict from a more extensive range during glacial epochs that might span several, perhaps many glaciations. Because very cold habitats in tropical zones have many fewer pathogens, predators, competitors (and food resources), species adapted to high-altitude habitats become exceptionally vulnerable when climates warm and they come into contact with species from lower altitudes. These bring contact with diseases to which the 'glacial species' have no resistance as well as being potential sources of competition for scarce food sources.

STATUS The local authorities in SW Tanzania are currently well aware of the global importance of their region and support initiatives to conserve Kipunjis. Although poaching and retribution for crop-raiding remain minor dangers, the greatest danger is probably diseases for which Kipunjis have no resistance.

BABOON-MANGABEYS *Lophocebus*

Grey-cheeked Mangabey	*Lophocebus albigena*
Black Mangabey	*Lophocebus aterrimus*

OTHER NAMES Fr. *Lophocèbes*. Ger. *Mantelmangabe*.

RECOGNITION Black or brown monkeys with very long tails and rather 'ragged', tesselated fur with tufts on the crown or brows. Their all-black faces display large, baboon-like incisors in a short, pointed muzzle above a receding chin. Deep suborbital pockets throw the very muscular cheeks (which are not hidden by fur) into strong relief. Their oblique eye sockets give them a somewhat mournful expression. Their deliberate movements, exaggerated postures, general demeanour and choruses of grunting are reminiscent of baboons.

GENEALOGY Baboon-mangabeys differ from drill-mangabeys in being almost wholly arboreal, living at high densities, and in the vocal repertoires of males. There are few fossils to indicate early origins but discovery of a new genus, *Rungwecebus* (initially allocated to *Lophocebus*) in SW Tanzania offers new insights into how *Lophocebus* might have evolved. Genetic analysis of *Rungwecebus* has revealed closer affinities with *Papio* than with *Lophocebus*. That affinity is consistent with its occupation of the south–east realm and the habitat within which it first differentiated. *Lophocebus*, now occupying the centre–west realm, has moved, with conspicuous success, into lowland rainforest, losing its putative association with mountains. What lends this evolutionary scenario some credence is that the very extensive (but little known) Marungu/Malimba/Mugila mountain complex, west of Lake Tanganyika, is immediately adjacent to the highland block within which *Rungwecebus* can be presumed to have differentiated from a *Parapapio*-like ancestor, possibly between about 3 mya and 2.7 mya. Less than 150km of L. Tanganyika's forested shores separate the two mountain blocks. The retreat of cool habitats during inter-glacials was more extensive near the Equator, providing opportunities for previously montane species to adapt to wholly tropical habitats.

GEOGRAPHY Primarily central African, their absence from Upper Guinea, yet supposed presence as fossils in upland East Africa implies Plio-Pleistocene origins, perhaps along the spine of the western (Albertine) Rift. The long chains of mountains west of L. Tanganyika might have been important diffusion centres for adjacent piedmonts and lowlands to absorb montane species during interglacials. Today *Lophocebus* species are lowland rainforest monkeys, with a preference for swamp forest that is most in evidence when many other monkey species are present.

ECOLOGY Although all mangabeys are dependent on being close to water, baboon-mangabeys are less riverine specialists (as *Cercocebus* seems to be) than nut and hard fruit specialists. Such fruits are picked at all levels, as, or before, they ripen.

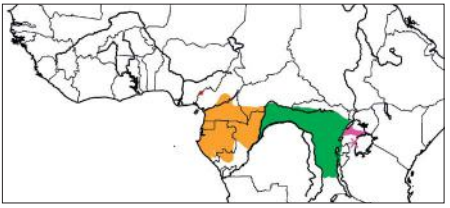
NATURAL HISTORY Baboon-mangabeys live at higher densities than drill-mangabeys (18–77 per km^2 as opposed to 6–12 per km^2). Less direct competition with guenons may influence this but their

social system consists of larger groups that depend on males as vocal (and often unseen) beacons for general orientation and inter-group avoidance. Thus adult males conserve energy that might otherwise have to be used to defend territories or harems. This strategy also reduces the need for physical expressions of dominance in males and, likewise, life in the tree-tops reduces the need for a protective role for males.

ADAPTATIONS Baboon-mangabeys are relatively small monkeys well suited to safe movement on smaller branches and efficient harvests of fruits and foliage. They show little difference in size between the sexes and no marked differences in the size of males or their muzzles. These characteristics have evolved without their having lost the big incisors and nut-cracking skills of their more terrestrial, larger, long-muzzled ancestors. The specialised air sacs that males have evolved to amplify their loud calls would appear to have replaced big muzzles as a primary feature of male self-advertisement.

GREY-CHEEKED MANGABEY

Lophocebus albigena

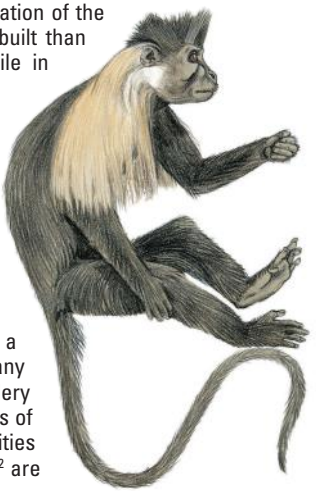


Grey-cheeked Mangabey

OTHER NAMES Fr. *Mangabey à joues grises*. Ger. *Grauwangen Mangabe*.

MEASUREMENTS HB 440–640mm (♀), 540–750mm (♂). T 570–940mm. W 4–7kg (♀), 6–11kg (♂).

RECOGNITION A dark-brown monkey with a long, ragged tail and tufted crown. A shoulder cape of longer paler fur in males varies in colour, both from individual to individual and regionally. The black face is naked and the cheeks only very thinly haired. The male's loud call is a very distinctive 'whoop gobble'. It is uttered several times a day and provides a clear indication of the presence of this mangabey. Females are more slenderly built than males and develop very conspicuous pink swellings while in oestrus.



GEOGRAPHIC VARIATION (sometimes treated as species):
L. a. albigena (central Africa): fawn or greyish cape.
L. a. johnstoni (E Congo, W Uganda): brown- to straw-coloured cape.
L. a. osmani (R. Cross): russet cape, pale underside.
L. a. ugandae (S Uganda): shorter mane, smaller head.

DISTRIBUTION From the Cross R. to the R. Nile north of the Cong R./R. Lualaba. Mainly lowland but recorded up to 1,600m in strictly equatorial zone.

HABITAT Rainforest, both primary and secondary, but with a strong preference for swamp forest (especially where many other monkey species are present). In one Uganda gallery forest, with only two marginally sympatric species, densities of 77per km^2 have been recorded. In the mixed primate communities of Cameroon and Gabon densities of 10–20 animals per km^2 are more usual.

FOOD Mainly fruits and nuts, notably false nutmeg (*Pycnanthus*), breadfruit (*Treculia*), dwarf dates (*Phoenix*) and oil palm (*Elaeis*). Shoots may be taken and roots dug for when fruits are scarce. Grey-cheeked Mangabeys feed for 3–4 hours after dawn and before dusk, with a short bout at midday, and rest in the late morning and afternoon.

BEHAVIOUR Social units consist of five or six females and their offspring, with several adult males, one of which is dominant. The dominant male is the most frequent caller and marks the position of his group relative to other neighbouring groups. Home ranges of about 4km^2 are non-territorial, with extensive overlaps between groups. Groups rest and sleep in a tight formation in a single tree or clump of dense foliage. Breeding is not seasonal and gestation lasts about 24 weeks. Males

take an active interest in young. Longevity is markedly affected by local variations in diet. Those consistently feeding on hard nuts wear out their teeth much faster than those with a softer, less restricted diet. The former tend to live in multi-species primate communities and show a faster turnover of population, including males.

ADAPTATIONS The air sacs and enlarged vocal tracts of male Grey-cheeked Mangabeys serve their special reliance on sound. As every male matures he elaborates an individual call-signature or 'gobble'. When a male becomes dominant within his group his call becomes the beacon for his entire group's movements and orientation.

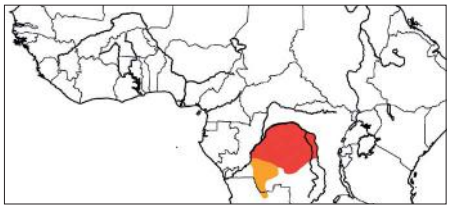
STATUS Although this species is very widely distributed and common within much of its very extensive range, agricultural expansion, hunting and tree-poisoning by foresters has caused local disappearances. Loud calls increase vulnerability but this is offset by its agility and arboreal skills.

BLACK MANGABEY

Lophocebus aterrimus

OTHER NAMES Fr. *Mangabey noir*. Ger. *Schopf Mangabe*.

MEASUREMENTS HB 450–650mm. T 800–850mm. SH 400–450mm. W 4–7kg (♀), 6–11kg (♂).



Black Mangabey

RECOGNITION A long-limbed, all-black monkey with a ragged, slightly prehensile tail, a pointed crest, and cheek-whiskers. Females are smaller and more slender than males, with pink sexual swellings during oestrus. Very closely related to the Grey-cheeked Mangabey, the Black Mangabey makes similar vocalisations, which probably serve similar social functions.

GEOGRAPHIC VARIATION

L. a. aterimus (central Congo basin): upswept sepia cheek-whiskers, conical crest.

L. a. opdenboschi (NE Angola and W DR Congo): sideswept black cheek-whiskers, ridged crest.

DISTRIBUTION Low-lying parts of the SW Congo basin.

HABITAT Moist rainforest, both primary and secondary, but especially swamp forests and their margins. Black Mangabeys utilise all levels but seldom descend to the ground.

FOOD Mainly fruits – similar to Grey-cheeked Mangabeys.

BEHAVIOUR Multi-male groups numbering 14–20 animals break down into smaller units while feeding. In some localities densities of nearly 70 animals per km^2 have been recorded. The variety of grunts suggests a complex web of social relations. Home-ranges may be smaller than those of Grey-cheeked Mangabeys but most parameters are very similar.

ADAPTATIONS The absence of any colour markings, deliberate movement and exaggerated postures suggests that the black silhouette of the animal is its most important visual signal. This relatively poor capacity for visual communication is offset by a very rich vocal repertoire.

STATUS Current status is insufficiently known. It is thought to be present in Salonga NP and is known from the proposed Lomako conservation area. It is hunted for meat in most parts of its range. Currently listed as Class B (African Convention) and Appendix II (CITES).

GELADA *Theropithecus*

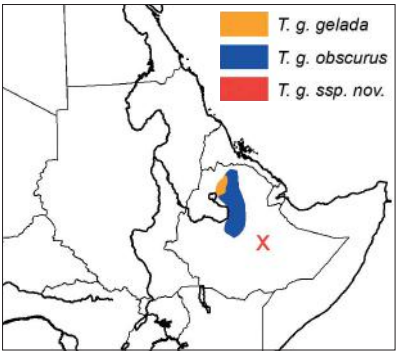
A monotypic genus with a single extant species, restricted to the Ethiopian highlands.

GELADA *Theropithecus gelada*

OTHER NAMES Gelada Baboon. Fr. *Gelada*. Ger. *Dschelada*, *Blutbrust Pavian*.

MEASUREMENTS HB 500–650mm (♀), 680–750mm (♂). T 320–640mm (♀), 450–550mm (♂). W 8.3–13.8kg (♀), 15.5–20.5kg (♂).

RECOGNITION Brown terrestrial monkey with thick fur, giving the impression of a heavy body on short limbs. Outer fur tassels of adult males often have a bleached appearance, especially on the head, chest, tufted tail and lower hindlimbs. Shoulders, hands and feet are very dark brown. Adult males develop a cape that envelops them to below the elbows and to the root of the tail. A deep prognathous lower jaw, retracted nostrils and concave muzzle give the face a dished look. This shortened upper muzzle allows the pink-lined upper lip to be retracted and everted, covering the entire upper muzzle in the brief 'gelada grin' display (see p.128).



Gelada

Females are smaller than males, more uniform in colour and coat length. Vesicles of pink sexual skin frame the genital area during oestrus. Similar vesicles (which also swell during oestrus) form an hourglass-shaped necklace framing the naked pink breasts of females. Males have a similar naked patch on the chest but without vesicles.

GEOGRAPHIC VARIATION A boundary between so-called *'T. g. gelada'* in the drier north and the darker *'T. g. obscurus'* in the moister south is probably impossible to draw. Another population in the Wabe Shebelle gorges might represent a distinct subspecies.

DISTRIBUTION Central Ethiopian plateau between Blue Nile Gorge and the upper Wabe Shebelle valley. Inhabit escarpments between 2,000 and 4,000m altitude.

HABITAT Feeds mainly on the flat margins of high grass plateaus (known locally as high Wurch or Puna grassland steppe), with *Agrostis* and *Festuca* grasses and giant *Lobelia* groves. Bands keep within 2km of the escarpment edges, where they retreat at night or at the least alarm. Ranges are therefore linear, encompassing as little as 1–3km^2 for a band's core area, although their year-long range may cover up to 70km^2. Steep cliffs provide sleeping-roosts.

FOOD Almost all the food comprises the leaves of grasses, which are plucked blade by blade with strong, neatly opposable thumb and fingers. Virtually all feeding is conducted seated and animals often shuffle from clump to clump without getting up (saving energy and conserving warmth is important for an animal that exists on an energy-poor diet in a cold climate). During dry seasons when there is heavy overgrazing by livestock, or when Gelada bands are very concentrated, subterranean stems and rhizomes are excavated, causing temporary devastations locally described as 'gelada fields'. Fruits and invertebrates are eaten opportunistically but are not a significant part of the diet. Where agriculture encroaches on the Gelada's habitat, cereal crops may be taken.

BEHAVIOUR Gelada bands are social units of 50–250 animals consisting of 2–30 harems (each led and controlled by a single adult male) and one or more bachelor groups. Bands cluster together on sleeping-cliffs and often feed and move in a single, dispersed scatter. They join up

Gelada, female showing sexual swellings

Gelada, female from the front

Gelada, male showing the 'lip flip'

with other bands from time to time and may aggregate into herds of up to 600 individuals. Members of a harem or band keep in touch with low-contact grunts and signal alarm with a high-pitched bark. Occasional violent outbursts among males elicit loud screams and distressed juveniles utter a prolonged wail. Breeding is seasonal, with most births falling between February and April. Gestation is about 6 months; the young are weaned at 2 years and mature sexually at 5 years (females) or 6–7 years (males).

ADAPTATIONS In spite of their long teeth, thick manes, ruffs and large size, male Geladas display obvious aggression only during contests over females. Nonetheless, intimidation or warning displays help regulate Gelada society. As with other baboons, ritualised yawning combines warning with appeasement but their unique 'lip-flip' constitutes an everyday greeting – a species-specific 'gelada-grin'.

Because harems are founded on force there would be a serious potential for disruptive aggression among the formidable-looking males. This danger is offset by an attractive, non-threatening signal. As with Sacred Baboons, male Geladas have evolved areas of naked skin that mimic female sexual skin. Unlike Sacred Baboons, however, this bare skin is not on the buttocks but on the chest, an area better suited to an animal that spends more time sitting down than standing. This vivid hourglass-shaped patch on the throat and breast of both sexes has earned the Gelada the English name 'bleeding-heart monkey'. The evolution of such complex mimicry suggests that sexual signs are important not only in reproductive behaviour but also in the regulation of social life. Chest patches make 'presentation' of the rear a redundant gesture and apparently represent a benign and attractive signal. The Gelada is a poor tree-climber but clambers over steep cliffs. Almost entirely terrestrial.

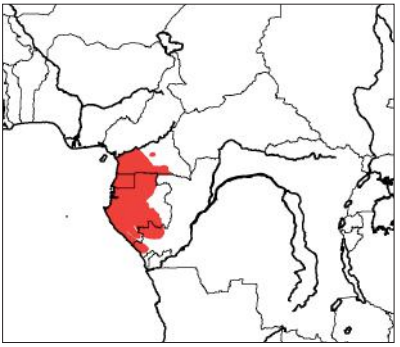
STATUS The fossil record indicates that six species of geladas became extinct during the last 3 million years. A combination of human predation, climatic change and bovid competition might account for their disappearance. Geladas were estimated to number 0.5 million in the early 1970s. They are still widespread but continuous agricultural expansion into their habitat is steadily eroding their overall range. They are shot as crop-pests and have been trapped as laboratory animals in the past. Selective shooting of adult males for their capes (as fur hats for sale to tourists or for local ceremonial costumes) has been shown to have reduced adult males in one locality from 9% to 2% of the total population. A few Gelada bands range within the minuscule Simen NP but there are proposals for a new Blue Nile Gorges NP and Indeltu (Shebelle) Gorges Reserve that might, hopefully, protect larger numbers.

T. g. gelada listed as vulnerable; *T. g. obscurus* of least concern (IUCN); Class A (African Convention), Appendix II (CITES).

MANDRILLS *Mandrillus*

Mandrill	*Mandrillus sphinx*
Drill	*Mandrillus leucophaeus*

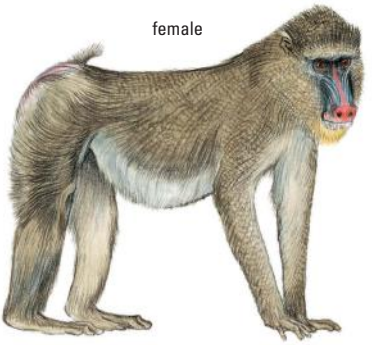
MANDRILL *Mandrillus sphinx*



Mandrill

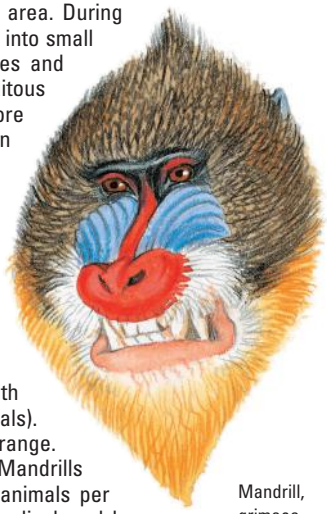
OTHER NAMES Fr. *Mandrill*. Ger. *Mandrill*.
MEASUREMENTS HB 550–700mm (♀), 700–950mm (♂). T 70–100mm. SH 450–500mm (♀), 550–600mm (♂). W 10–15kg (♀), 19–30kg (♂).
RECOGNITION A heavily built baboon with a grizzled olive-brown coat, pointed orange beard, crested crown and dull white to grey underside. In males the bare face and posterior are bright red, white and blue. Males have two swollen nasal ridges which are electric blue and grooved, giving the impression of a permanent snarl. White fur surrounds the red-lipped mouth and forms leaf-shaped flashes behind the flesh-coloured ears. A red midline runs between the nasal arches, culminating in a circular scarlet nose-patch. Other scarlet areas include the penis and a circle around the anus. Adult males are stocky and the great width and muscularity of their buttocks is emphasised by their being naked and coloured pink above and blue below (graduating through mauve). Females are half the size and weight of males; their faces are flatter and shorter with grooved, pale blue ridges on the muzzle and a pink mouth and nose.
DISTRIBUTION Central W Africa from R. Sanaga to Congo R. inland to R. Ivindo and R. Ogooué. Mandrill distribution follows moist evergreen forest where this high-density, social animal can find bulk forage throughout the year. A prime need is abundant herbaceous growth to buffer it while fruits are scarce.
HABITAT Primary evergreen rainforest, stretching between 100 and 300km inland from the Atlantic coast. In this forest the fruiting of trees and lianas is irregular, resulting in periodic shortages of fruits. Undergrowth is typified by extensive patches of perennial herbs, such as gingers (Zingiberidae)and arrowroots (Acanthaceae), notably *Brillantaisia* and *Phaulopsis*. Within this zone the secondary growth that follows logging, settlement and shifting cultivation is also used by the Mandrill.
FOOD Omnivorous, with fruits preferred whenever they are available. In the course of a year groups of Mandrills are thought to range over an area of about 50km^2. They forage very intensively in a succession of small subsections, exhausting local resources over variable amounts of time (but on average moving on about once a month). Size of foraging groups depends

male



female

on extent to which food resources are scattered within an area. During seasons in which many trees are fruiting, Mandrills disperse into small social units. When fruits become scarce they turn to leaves and herbaceous growth. At such times a less nutritious but ubiquitous food supply permits temporary mega-groups, numbering more than 600 animals, to form. These hordes supplement their main diet with herb stems and leaves, roots, fungi, invertebrates including crabs and snails, and occasionally vertebrates – frogs, lizards, rodents, even young duikers. Foraging in large congregations is mostly terrestrial but fruits are sought wherever they can be found, including in the canopy.



Mandrill, grimace

BEHAVIOUR Smallest social unit is an extended harem led by a single dominant male. In groups with two or more males, subordinate individuals establish size hierarchies (subordinate status revealed in slimmer proportions and duller colouring). Harems consist of juveniles and infants with up to 20 adult females (average total harem about 30 animals). Harems readily join up with other harems within their home-range. Aggregated harems may incorporate 10 or more harems. Mandrills walk 5–15km in a day. Densities in undisturbed areas 5–7 animals per km^2. Single animals uncommon, often old males presumably displaced by fighting. Adult males estimated at only 7% of total population, suggesting heavy casualties during fights for control of harems.

Small groups of Mandrills may forage silently but bands or clans emit a continuous chorus of two-phase barks, frequent 'crowing', grunts and squeals. Sleep in trees but always travel on the ground.

Gestation lasts about 25 weeks and sexual maturity is reached in about 5 years. Full maturation in subordinate males appears to be inhibited by the harem-master's presence. Captive specimens have lived for up to 47 years. Some breeding continues all year round but there appear to be peak breeding times, with births 1 or 2 years apart. Harem-masters monopolise mating of oestrous females, identifiable by their pink- and violet-mottled sexual swellings.

ADAPTATIONS Ritualised yawns express tension and possibly a form of appeasement. Among Mandrills most frequent greeting is a low-intensity yawn, opening the corners of the mouth with wagging of the head. Mandrill facial features accentuate impact of such gestures, especially the nasal folds, which appear to mimic a snarl with their enlarged and brilliantly enhanced creases. The size and brilliance of the nasal folds accurately reflect the age and condition of a male Mandrill, thus allowing other individuals to make an instant assessment of his rank. In a densely obstructed, poorly lit forest environment this signal is unambiguous and highly specific.

STATUS Destruction and degradation of evergreen forests in many areas reduces the capacity of environments to support Mandrill populations. However, commercial bushmeat hunting poses the most immediate threat. Researchers have recorded far fewer contacts with Mandrills in recent years. It appears to be most seriously endangered in Congo (Brazzaville). Listed as Class B (African Convention), Appendix I CITES lists as vulnerable.

DRILL *Mandrillus leucophaeus*

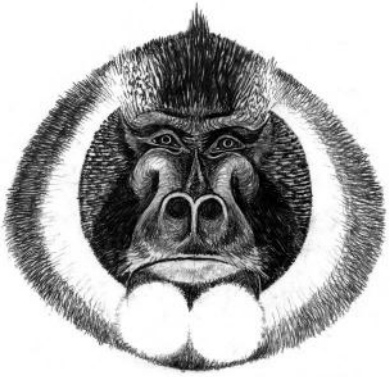
OTHER NAMES Fr. *Drill*. Ger. *Drill*.

MEASUREMENTS HB 450–620mm (♀), 580–1,080mm (♂). T 60–120mm. SH 450–500mm (♀), 550–600mm (♂). W 6.5–20.5kg (♀), 14.5–45kg (♂).

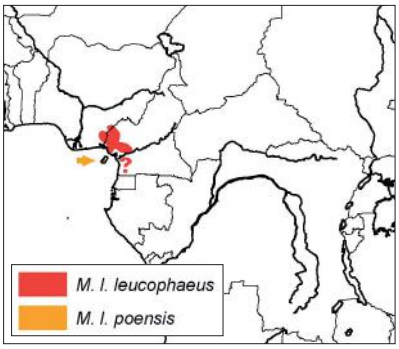
RECOGNITION A stocky, large-headed olive-brown baboon with an off-white underside and a broad, leaf-shaped white ruff surrounding a naked black face. A dense neck-cape serves to greatly enlarge the visual impact of the adult male's head and chest. Below the stumpy tail the broad, bare buttocks resemble those of the Mandrill, especially in the adult male. Pink, graduating to blue with extensive metallic mauve, they top a scarlet scrotum. Hands and feet resemble those of the Mandrill in being broad and strong. The hind big toe or 'foot thumb' is particularly well developed.

GEOGRAPHIC VARIATION *M. l. leucophaeus* (mainland), *M. l. poensis* (Bioko I.).

DISTRIBUTION Moist evergreen forest on Bioko I. and between the Cross R. and R. Sanaga valleys. Limitations to the Drill's range are likely to be similar to those that affect the Mandrill.

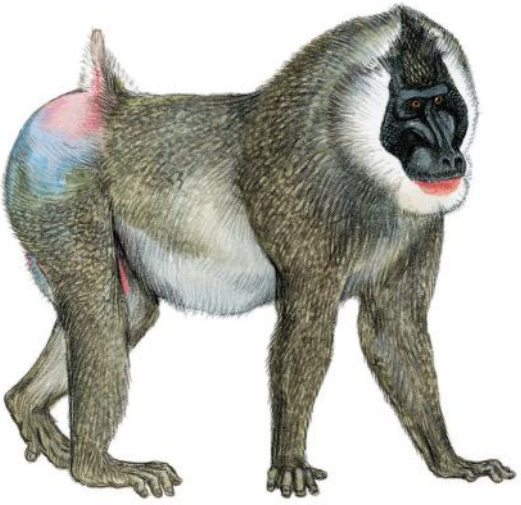


Drill, adult male facial geometry

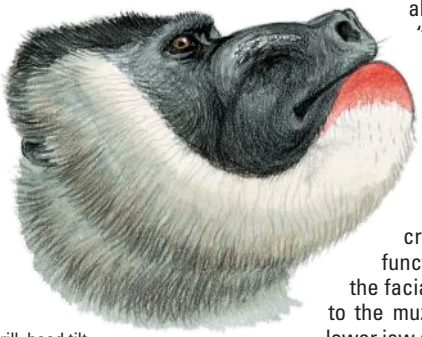


Drill

HABITAT Evergreen forest on littoral and in Cameroon mountains up to 1,000m; also forest–savanna mosaics. Drills have also been noted in rocky areas within the forest.
FOOD Omnivorous with reliance on fruit staple; also much herbaceous growth, roots, mushrooms, invertebrates (notably worms, termites, ants and spiders) and small vertebrates. Seasonal changes in diet unlikely to differ greatly from those of the Mandrill. Giant land snails, coconuts and sea turtle eggs have been recorded. Disabled duikers infrequently eaten.
BEHAVIOUR Social structure resembles that of Mandrills. Basic units are harems of up to 25 Drills, periodically coming together to form bands numbering up to 200 animals. Smaller numbers in these units may reflect Drills' lower densities. Males remain in harems, except for a few presumed expellees who wander alone. Groups travel on the ground but forage and sleep in trees. Drills utter sharp alarm barks and grunt while foraging. Also a distinctive crowing call that typifies contact between harems. Distressed juveniles make a croaking call. Dominant males' threat displays involve much branch-shaking and head-bobbing. Breeding continuous but births spaced up to 6 years apart. Reproductive tempos and maturation rates similar to those of the Mandrill.
ADAPTATIONS Adult male Drills and Mandrills have chest glands, regularly rubbed on branches or tree trunks. Scent-marking increases 'ambience' of a harem-master's presence among other harem members and thus reinforces his role as a physical, visual, auditory and olfactory beacon in a highly mobile, non-territorial but easily dispersed social unit. Because the dominant male initiates



Drill, adult male


Drill, head tilt

all movements and his own actions elicit a strong 'follow' response in his harem members, his rump has a role as a beacon. Its brilliance and breadth is a clear sign of status while atrophy of the tail probably eliminates ambiguous or distracting signals (the same is probably true of the Mandrill).

A ritualised 'smile' that displays the teeth is often combined with tilting of the head. A vivid crimson lower lip accentuates this gesture, which functions as a greeting or appeasement. Whereas the facial features of the Mandrill draw attention mainly to the muzzle, the signal given by Drills emphasises the lower jaw and overall enlargement of the head by means of concentric circles of black, white and grey. Head-tilting makes the open lips and teeth more prominent and visible.

STATUS Drills are in danger of becoming extinct. In the heart of their range, between Douala and Edea, they have been totally exterminated by clear-felling for chipboard factories and settlement. Hunted everywhere for their meat, it is common for all the members of a harem who have taken refuge in the trees to be shot en masse. As cultivation expands, Drills are frequently killed in defence of crops. Remaining populations in SW Cameroon, Korup NP and southern corner of Bioko I. IUCN rates as endangered. Listed as Class B (African Convention), Appendix I CITES lists as endangered.

DRILL-MANGABEYS *Cercocebus*

Golden-bellied Mangabey	*Cercocebus chrysogaster*
Red-capped Mangabey	*Cercocebus torquatus*
White-naped Mangabey	*Cercocebus lunulatus*
Sooty Mangabey	*Cercocebus atys*
Agile Mangabey	*Cercocebus agilis*
Tana River Mangabey	*Cercocebus galeritus*
Sanje Mangabey	*Cercocebus sanjei*

RECOGNITION Sometimes known as white-eyed mangabeys or 'eyelid monkeys', because of their white upper eyelids, these longer-muzzled monkeys were formerly classified together with the Black Mangabey, which is more arboreal, longer tailed and shorter muzzled. The West African species have the longest muzzles and are smoky-grey in colour. Those from central and East Africa are smaller, with shorter muzzles and browner, more grizzled coats. Pockets, or fossae, between the eyes and corners of the mouth are distinctive in both types of mangabey.

GENEALOGY Fossils from southern and East Africa, if correctly identified, suggest that mangabeys might have been commoner and more widespread between 4 million and 2 mya. They are now exclusively equatorial. Studies of their anatomy, blood proteins and chromosomes suggest that their closest affinities are with mandrills. A retracted position for the muzzle in relation to the rest of the skull suggests that they derive from a larger, longer-faced ancestor.

GEOGRAPHY The contracted and fragmented distribution of drill-mangabeys suggests that their present status is but a vestige of what it was in former times. This decline is unlikely to be the result of human interference and may be the consequence of a long period of subtle competition with, and displacement by, guenon monkeys and baboons, which they most closely resemble.

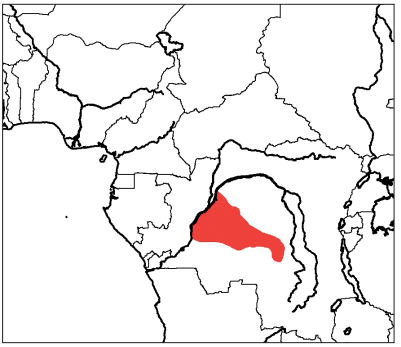
ECOLOGY Rivers and swamps often represent vestigial islands of water-dependent vegetation remaining in the wake of climatic changes that have brought drier communities elsewhere. Both within and outside the forest belt drill-mangabeys are consistently riverine species but might be considered more of a 'vestigial' group in comparison to other swamp-forest specialists.

NATURAL HISTORY All drill-mangabeys live in multi-male, multi-female groups where competition among members of both sexes may be sharper between neighbouring bands than within the immediate group. Differences between the sexes in size and morphology are therefore much less

extreme than in Drills and baboons. A reduction in overall size (especially in the canine teeth) would help explain the facial pockets, or fossae, which may be the result of buckling in the plane of junction as a once extended muzzle contracted (over a relatively short period of evolutionary time).
ADAPTATIONS Both Drills and drill-mangabeys derive from lineages that moved into moister galleries and forests from drier, more open habitats. In spite of this they remain relatively terrestrial, a conservative habit that may render them less able to compete with the guenons. The robust molar teeth of drill-mangabeys enable them to cope well with nuts and hard fruits typical of their riverine ecotype. In addition, drill-mangabeys show an ability and a willingness to swim.

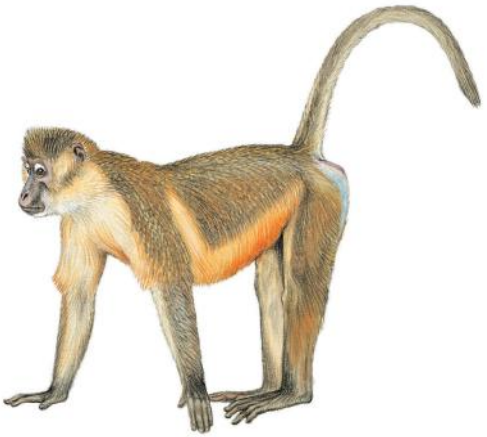
GOLDEN-BELLIED MANGABEY

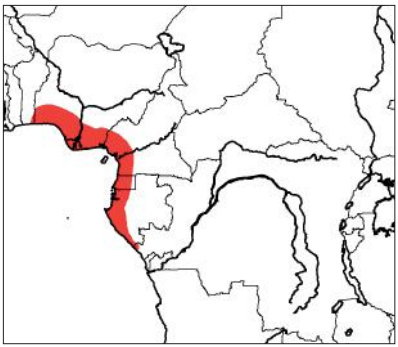
Cercocebus chrysogaster



Golden-bellied Mangabey

OTHER NAMES Fr. *Cercocèbe à ventre doré*. Ger. *Goldbauch Mangabe*.
MEASUREMENTS HB 450–550mm (♀), 520–660mm (♂). T (est.) 500–750mm. SH 380–420mm (♀), 420–460mm (♂). W 6–8kg (♀), 10–14kg (♂).
RECOGNITION The most Drill-like of the drill-mangabeys in having a naked violet rump, bright-coloured fur and relatively robust build (including the muzzle of adult males). The crown, back and outer limbs are a rich, dark, grizzled olive. The underside is cream, turning to bright orange on the belly. The cheek-whiskers are swept out into a prominent ridge that begins near the corner of the mouth and ends behind the ears. Below the temples the whiskers form a golden-yellow furrow that frames the upper face like a high collar. The tapered tail is carried in a backward arch (unlike other mangabeys).
HABITAT Restricted to the southern (lower) section of the Congo depression swamp complex, the Golden-bellied Mangabey's environment resembles that of the Agile Mangabey living immediately north of the Congo R. Nonetheless, their separation could be quite ancient, not only because of the sheer width and speed of the river in its lower reaches. It could date back to times when the basin was a lake.
FOOD Presumed to be mainly fruits, such as figs, sugar plums, dika nuts, raphia and dwarf date-palms.
STATUS Least known of the mangabeys, this species occupies an area where hunting is intensive. Nonetheless, its swampy habitat is likely to protect satisfactory numbers for the time being. It occurs in Salonga NP. (Currently classed in conservation inventories as a subspecies of *Cercocebus galeritus*.)





Red-capped Mangabey

RED-CAPPED MANGABEY

Cercocebus torquatus

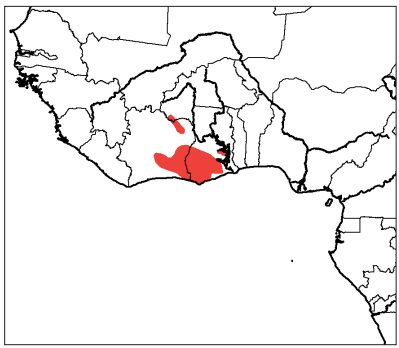
OTHER NAMES White-collared Mangabey. Fr. *Cercocèbe à collier blanc*. Ger. *Rotkopf Mangabe*.
MEASUREMENTS HB 450–600mm (♀), 470–670mm (♂). T 600–750mm. SH 380–420mm (♀), 400–450mm (♂). W 5–8kg (♀), 7.0–12.5kg (♂).
RECOGNITION A large slate-grey monkey with white underside and inner limb surfaces. The dark grey tail is frequently held so that its white tip hovers over the head, which is bisected laterally by a boldly outlined ridge of fur running from cheek to neck. Large blackish ears project from the white collar that surrounds a bright russet cap. White eyelids are particularly conspicuous in the long-muzzled, dark face.

The metallic-sounding cackles and alarm barks of this species are very loud and are accompanied by much branch-shaking and grimacing by the adult males. Several adult males are present in the larger groups, which number between 12 and 23 animals, but subgroups readily form. Rolling calls preceded by a whoop signal the positions of neighbouring groups and individuals.
HABITAT Seldom far from swamp or valley forest, but the dry-season range may expand as fruits become scarcer and less concentrated. Occupies region between Cross R. to Ubangui/Congo rivers.
FOOD Mainly fruits and nuts, supplemented by the stems and roots of undergrowth plants. Seasonal fluctuations in foraging behaviour ensure substantial overlaps between neighbouring groups.
STATUS Once a successful and widespread species, the Red-capped Mangabey is nonetheless incompatible with intensive cultivation and is disappearing from all areas where agricultural expansion is being consolidated. It is intensively hunted, especially in Cameroon and Nigeria. Listed as Class B (African Convention), Appendix II (CITES), IUCN rates as vulnerable.

WHITE-NAPED MANGABEY *Cercocebus lunulatus*

OTHER NAMES White-crowned Mangabey. Fr. *Cercocèbe couronne*. Ger. *Weibcheittel Mangabe*.
MEASUREMENTS HB 520–560mm (♀), 520–730mm (♂). T 680–740mm. SH 380–420mm (♀), 400–450mm (♂). W 3.9–6.3kg (♀), 7.1–11.8kg (♂).
RECOGNITION A brownish-grey monkey with an off-white underside and prominent, tufted white nape. There is a narrow black midline down the entire length of the grey back: the outer surfaces of all limbs are also grey, hands and feet are a darker grey. Facial skin is brown on the muzzle, pinkish around the orbits, and the upper eyelids are white.

Formerly treated as a subspecies of *C. atys* or *C. torquatus*, or as a hybrid between the two, it is now thought more likely it represents the descendant of a population ancestral to both the other species.



White-naped Mangabey

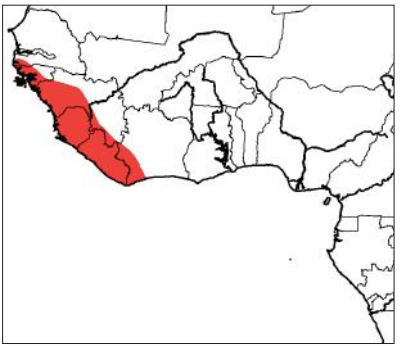
The commonest calls have been described as chirps, grunts and 'karakoo' barks. In common with other mangabeys, an attention-getting whoop is followed by a loud gobble. Duetting gobbles between separate groups probably served to space out such groups. As with other species, eyelids are flashed during direct confrontations.

HABITAT Once ranged between the Volta and Nzo-Sassandra rivers but in a progressively more fragmented distribution. They were commonest in coastal mangrove, swamp and *Raphia* palm forests, but formerly were also found in primary and secondary forests before most were felled.

FOOD Feeds at all levels of the forest but preferentially on the forest floor where it finds a variety of fruits and seeds, both ripe and unripe.

STATUS White-naped Mangabeys have been and continue to be hunted intensively throughout their range to the point where they have become one of the most endangered of all African primates. It has been estimated that as few as 1,000 individuals may survive. IUCN rates as endangered.

SOOTY MANGABEY *Cercocebus atys*



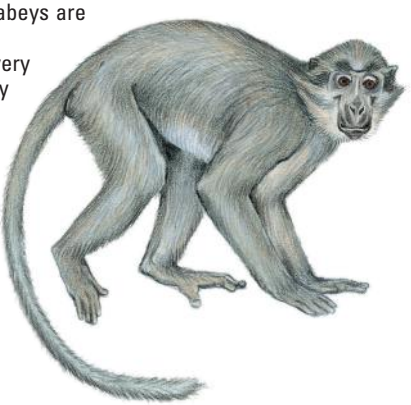
Sooty Mangabey

OTHER NAMES Smoky Mangabey. Fr. *Cercocèbe fuligineux*. Ger. *Mohren Mangabe*.

MEASUREMENTS HB 450–600mm (♀), 470–670mm (♂). T 400–800mm. SH 380–420mm (♀), 400–450mm (♂). W 4.5–7.0kg (♀), 7–12kg (♂).

RECOGNITION A smoky- or slate-grey monkey with a lighter underside and facial whiskers (white-collared with greater contrast in eastern race) and slightly darker hands and feet. The bare facial skin is dark grey or mottled, the upper eyelids are white and the orbits and muzzle are 'rectangular' in outline. The Sooty Mangabey is often more easily heard than seen. The commonest calls are a staccato bark, a rapid succession of grunts and a whoop followed by a many-syllabled rumble; a rattling scream signifies alarm. Facial expressions are varied and eyelids are flashed a lot, especially in threat.

HABITAT Restricted to Upper Guinea between the Sassandra and Casamance Rivers, ranging along valleys within remnant primary and secondary forests out into gallery forest and mosaic zones. Sooty Mangabeys are commonest close to swamp and palm forests.



FOOD Fruits, including the flesh and kernels of very hard fruits and nuts, are the main staple. Sooty Mangabeys also eat the leaves, stems, shoots and roots of many swamp plants and the seeds of grasses. They frequently raid farms, including rice paddies, where damage can be extensive.

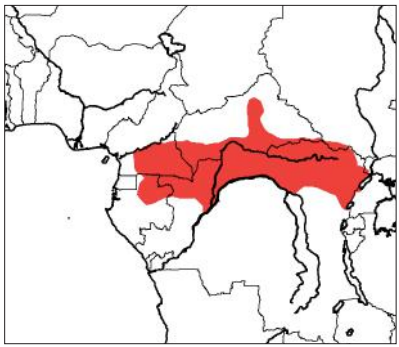
STATUS Until recently, Sooty Mangabeys were still widespread in West Africa, partly because they were difficult to hunt in their dense, swampy refuges. However, they are easy to trap because of their ground-foraging habits. They are treated as vermin in many pioneer agricultural areas. Categorised by IUCN as near threatened.

AGILE MANGABEY *Cercocebus agilis*

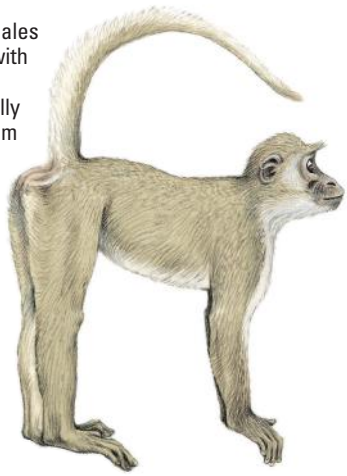
OTHER NAMES Fr. *Cercocèbe agile*. Ger. *Olivmangabe*.

MEASUREMENTS HB 440–550mm (♀), 510–650mm (♂). T 450–790mm. SH 370–420mm (♀), 400–450mm (♂). W 4.3–7.0kg (♀), 7–13kg (♂).

RECOGNITION A drab, speckled olive monkey with short, fine fur. The underside and inner limbs are pale and very thinly furred. The tail is tapered. The darker, grizzled crown has a parting at the front which often exposes a naked pale-coloured forehead behind a projecting brow tuft. The upper eyelids are scarcely paler than the pale grey face. The Agile Mangabey is more often heard than seen; its loud call is a whoop followed by a rumble which is made by the male. Groups numbering up to 18 are led and defended by a single adult male. Single males are common. Group encounters are often amicable, with occasional exchange of members.



Agile Mangabey



HABITAT Endemic to regions north of the Congo R., especially to the extensive swamp forests that follow the Equator from the Atlantic to eastern DR Congo. In areas where this type of vegetation follows narrow creeks and rivulets the habitat is essentially linear because the Agile Mangabey seldom moves out of seasonally flooded swamp forest. During dry seasons more time is spent on the ground but most activity is restricted to within some 5m from the ground, only adult males climbing to higher levels.

FOOD Almost entirely, certain dominant swamp-forest trees (notably dika nuts or Gabon chocolate, *Irvingia*, and sugar plums, *Uapaca*) for the period in which they are fruiting. Another dominant species, the *Raphia* palm, provides fresh leaf shoots that can buffer any shortage of fruits. Some 42 species of fruits have been recorded in the diet, with grasses, mushrooms and animals making up more marginal foods.

STATUS There are substantial overlaps between the diet of the Agile Mangabey and that of other monkeys, especially the De Brazza's Monkey. The Agile Mangabey is only half as numerous as any of the guenon species with which it shares its habitat, but its larger size and ability to fall back on *Raphia* shoots or harder foods in times of shortage may make it competitive within the swamp ecotype. Dense vegetation and treacherous ground protect the Agile Mangabey from predators, including humans. IUCN regards this species as of least concern but current unregulated bushmeat hunting is ultimately unsustainable.

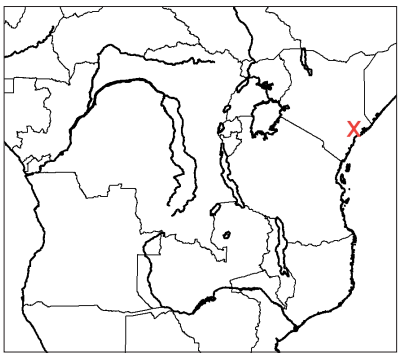
TANA RIVER MANGABEY

Cercocebus galeritus

OTHER NAMES Fr. *Cercocèbe de la Tana*. Ger. *Tana Mangabe*.

MEASUREMENTS HB (est.) 420–530mm (♀), (est.) 500–630mm (♂). T 450–770mm. SH (est.) 350–410mm (♀), (est.) 400–440mm (♂). W (est.) 5.0–6.5kg (♀), (est.) 8–10kg (♂).

RECOGNITION A grizzled ash-coloured monkey with limp, shaggy fur, prominent white eyelids, a flash of paler fur on the temples and white borders to the black face. Hair on the crown is particularly long and



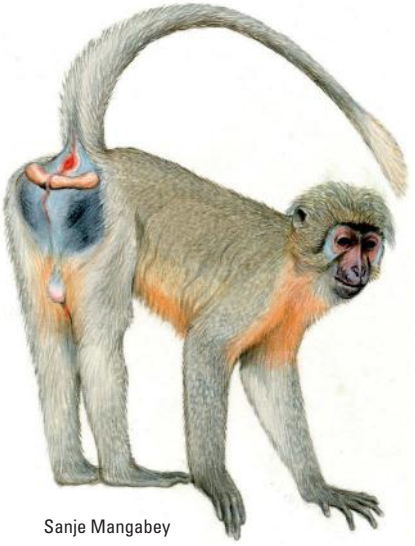
Tana River Mangabey

limp. The hands and feet are dark brown and the tail has an off-white tip that is somewhat tufted in adult males. Males vocalise with the whoop-rumble typical of all drill-mangabeys. Unlike the Agile Mangabey, groups of 13–36 contain up to six adult males. Two or more of these units occasionally aggregate to form temporary bands of up to 60 monkeys. It is semi-terrestrial, especially during the dry season.

HABITAT Restricted to gallery forests along the flood-plain of the R. Tana in Kenya, a zone only 60km long and nowhere more than a few kilometres wide. The preferred vegetation type is levee forest dominated by *Pachystela* but the Tana River Managabey also ranges into drier *Acacia/Mimusops* riverine strips. Surrounded by open grassland, which is regularly fired, it occupies a strictly finite environment centred on the Nkanjonja forest.

FOOD Mainly fruits, of which figs are especially important. However, the restricted nature of the habitat may mean that a larger proportion of seeds and animal foods are taken, including insects, frogs and lizards.

STATUS This species was estimated to number about 2,000 in 1972. In 1995 the estimate was 1,100 or fewer. Today the species is on the brink of extinction. Obvious threats are forest clearance (especially the felling of figs and other food trees for canoes), forest fires and degradation due to livestock and an artificially lowered water-table. A Tana River Primate Reserve has been officially degazetted, part of an overall contraction and degradation of all natural habitats in the Tana Delta. Irresponsible damming and irrigation projects for development aggravate an already critical situation. Listed as Class A (African Convention), Appendix I (CITES), endangered (IUCN).



Sanje Mangabey

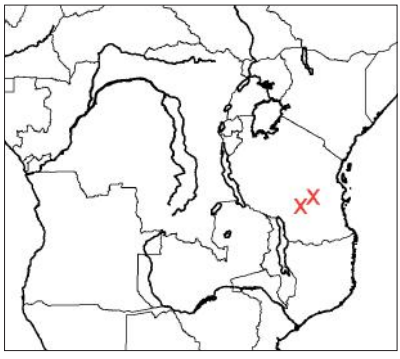
Tana River Mangabey

SANJE MANGABEY *Cercocebus sanjei*

OTHER NAMES Fr. *Cercocèbe de Sanje*. Ger. *Sanje Mangabe*.

MEASUREMENTS HB (est.) 500–650mm. T (est.) 550–650mm. SH (est.) 400–500mm. W (est.) 7–9kg.

RECOGNITION Crown, back, limbs and tail are a fine ash-grey grizzle. Hands and feet are darker. Belly and chest pale apricot to cream and there is a tufted off-white tip to the tail. Lank crown hairs droop either side of an ill-defined central parting. A very narrow black margin separates brow and cheeks from the paler face. The outer cheek skin is pale



Sanje Mangabey

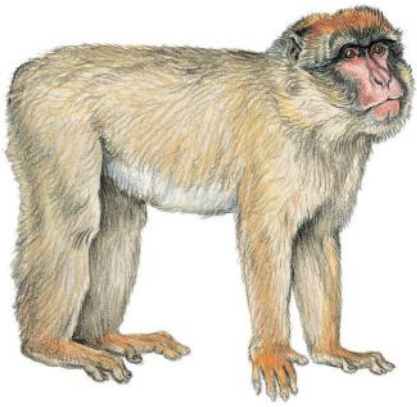
blue-grey and the orbits and upper muzzle are pink (eyelids not strikingly white). The lower muzzle is grey. Bare buttocks are bluish grey with narrow pink callosities. The penis and anus are vividly scarlet and the scrotum is pink and blue. Vocalisations include slow, deep, paired hoots followed by more rapid and croaking hoots, sudden very deep groans and sharp, shrill cries when excited.
HABITAT Valley forests on the wetter eastern flanks and below the Uzungwa (African Ghats) massif from 400–1,230m altitude. Although the Sanje Managabey ranges through several forest and woodland types, it prefers the lower understorey in riverine galleries.
FOOD Fruits, mostly ripe, comprise 70% of the diet while foliage makes up most of the balance. In an item-by-item comparison the diet shows very little difference from that of the guenons that share their habitat (e.g. *Cercopithecus mitis*). The guenons have the advantage of superior arboreal skills and larger numbers. The Angola Colobus (*Colobus angolensis*) also shows some overlap with foods favoured by the Sanje Mangabey.
STATUS The likelihood that long-term competition from guenons and colobus monkeys have reduced this mangabey to its present relict distribution makes it imperative that the ecological richness that allowed its survival at Sanje and Mwanihana be fully studied and conserved. Current proposals for an Uzungwa National Park may ensure this objective but widespread pit-sawing and charcoal burning is continuing to degrade these forests. Hunting with dogs (to which this monkey is particularly vulnerable) is also spreading as the area becomes more densely settled. In 1981 Sanje Mangabeys were estimated to number between 1,800 and 3,000 animals. Listed by IUCN as endangered.

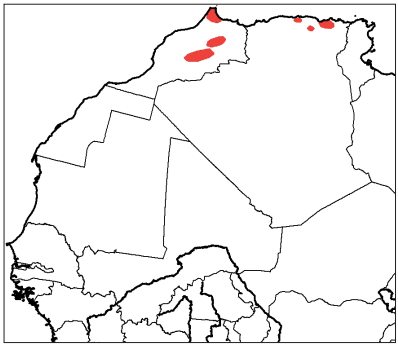
MACAQUES *Macaca*

A genus of Old World monkeys with just a single extant African species.

BARBARY MACAQUE *Macaca sylvanus*

OTHER NAMES Barbary Ape. Fr. *Magot*. Ger. *Berberaffe*.
MEASUREMENTS HB 540–560mm (♀), 600–750mm (♂). W 8–12kg (♀), 10–18kg (♂).
RECOGNITION A dull ochre-grey monkey with variable intensities of orange tinting the crown, hands and feet. Darker flushes of brown or black surround the bare face, which is pink or mottled. Hands short, broad, small thumb. Limbs of equal length, appear thick because of dense, woolly hair (especially in winter). Oestrous females have prominent swellings of sexual skin on their buttocks.
DISTRIBUTION Formerly ranging from Libya to Morocco (and in SW Europe in prehistoric times), the Barbary Macaque is now restricted to the Middle Atlas Mts and a scatter of localities in Morocco and Algeria. It ranges from sea level up to 2,000m.
HABITAT Cedar forests at higher altitudes presently preferred but contraction of the range mainly due to expansion of human settlement in more favourable areas. Also occurs in oak forests, coastal scrub and overgrazed rocky slopes with vestigial vegetation. Home ranges vary from 25 to 1,200ha.
FOOD In cedar forests, grass and cedar leaves are winter and spring staples, with acorns, caterpillars and daffodil (*Asphodelus*) bulbs the main summer and autumn foods. In deciduous oak forests, seed and acorn staples last from June to November while grass, lichens and bark see the





Barbary Macaque

macaque through the winter. A brief flush of caterpillars between April and May is important, as may be scarcer invertebrates, roots, bulbs and fungi.

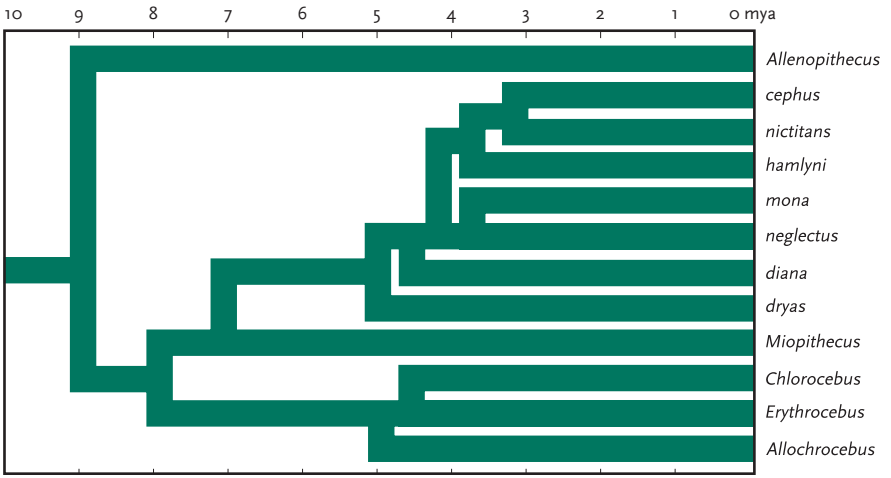
BEHAVIOUR Groups of 7–40 individuals (usually 10–30), comprising adults and young of both sexes, maintain contact with one another using a wide range of vocalisations. Young are born February to June after 7 months' gestation. Males pay much attention to infants. Adult males cooperate in defending the group and will even attack dogs. Sexually mature at about 4 years; life-span about 20 years.

ADAPTATIONS The African species is the most terrestrial of all macaques, spending more than half of its time on the ground. Occupation of dry, cool, impoverished habitats goes back at least 6 million years and represents a primary adaptation of cheek-pouched monkeys, not the late and marginal offshoot of an arboreal, tropical monkey, as is often assumed. These primary adaptive characteristics make conservation and further study of this species especially important.

STATUS Of all surviving Barbary Macaques, most are found in the Middle Atlas Mts in Morocco. Others persist in numerous pockets of declining size in N Morocco and Algeria. The main threat to their survival is intensive logging, charcoal-burning, firewood-collecting and land clearance for agriculture at lower altitudes. Degradation of the remaining areas by livestock also affects their long-term future. In Morocco it occurs in the Toubkal NP and Thassem Reserve. In Algeria it survives in the Djurdjura, Taza, Chrea and Gouraya NPs. There have been proposals to reintroduce it to the Kouf NP in Libya. Listed as Class A (African Convention), Appendix II (CITES), endangered (IUCN).

GUENONS AND ALLIES *Cercopithecini*

Allen's Swamp Monkey	*Allenopithecus nigroviridis*
Talapoins	*Miopithecus* group (2 species)
Patas Monkey	*Erythrocebus patas*
Savanna monkeys	*Chlorocebus* group (5 species)
Mountain monkeys	*Allochrocebus* group (3 species)
Dryad monkeys	*Cercopithecus (dryas)* group (2 species)
Diana monkeys	*Cercopithecus (diana)* group (2 species)
De Brazza's Monkey	*Cercopithecus neglectus*
Mona monkeys	*Cercopithecus (mona)* group (6 species)
Long-faced monkeys	*Cercopithecus (hamlyni)* group (2 species)
Gentle monkeys	*Cercopithecus (nictitans)* group (2 species)
Cephus monkeys	*Cercopithecus (cephus)* group (6 species)



Tentative phylogenetic tree for the guenons Cercopithecini.

Schematic illustration of coloured visual signals transmitted by several species of guenons (Cercopithecini). *Top, left to right:* Putty-nosed Monkey *Cercopithecus nictitans.* Diana Monkey *Cercopithecus diana.* Red-eared Monkey *Cercopithecus erythrotis.* Crowned Monkey *Cercopithecus pogonias.* Wolf's Monkey *Cercopithecus wolfi.* *Middle, left to right:* De Brazza's Monkey *Cercopithecus neglectus.* Diana Monkey *Cercopithecus diana.* De Brazza's Monkey *Cercopithecus neglectus.* Diana Monkey *Cercopithecus diana.* *Bottom, left to right:* Owl-faced Monkey *Cercopithecus hamlyni.* De Brazza's Monkey *Cercopithecus neglectus.* L'Hoest's Monkey *Allochrocebus lhoesti.* De Brazza's Monkey *Cercopithecus neglectus.*

RECOGNITION Guenons are medium-sized to small monkeys with long tails and grizzled fur on the back or limbs. Their colouring, particularly on the face, sometimes rivals that of birds for its brilliance and complexity of pattern. Although males of some of the more terrestrial species have relatively long muzzles and canine teeth, most have short faces and reduced molars. Two forms, *Allenopithecus* and *Miopithecus*, retain some prominent ancestral features more typical of macaques (such as 'pinched' molar cusps and enlarged sexual swellings in oestrous females) but are otherwise like guenons. The convention of associating Allen's Swamp Monkey and the talapoins with guenons is a convenience. They could equally well be treated as equatorial macaques.

GENEALOGY Guenons share a common ancestry with other cheek-pouched monkeys, baboons and macaques which diverged from the colobines over 13–18 mya. A near-absence of guenon fossils suggests that their earliest forebears inhabited minor regional niches within fossil-poor forest zones for a long period before exploding into the largest and most recent of all known primate radiations. Genetic studies have begun to chart this radiation. These studies indicate that patas, talapoin, savanna and forest-floor (*lhoesti*) monkey lineages form a distinct, mainly terrestrial branch while a second, more wholly arboreal, branch comprises two single species and five species-groups, embracing a total of 20 species and about 46 subspecies. How this bifurcation relates to Africa's many climatic oscillations from cold/dry to warm/wet awaits further research. Guenons vary greatly in the number of genetic changes they have accumulated. Thus, gametes of the recently evolved Crowned Monkeys (with 72 chromosomes) are much more diverse than those of Allen's Swamp Monkey (with 48 chromosomes). Species with very diverse face patterns (such as the Red-tailed Monkeys of the *cephus* group) all have sets of 66 chromosomes while the *mona* group, with 66–72 chromosomes, are genetically diverse in spite of their close resemblances. This

implies that monkeys of the *cephus* group have diverged very recently (and are, strictly speaking, nested within the older, more diversified *nictitans* complex). The *mona* group's evolution, instead, has been more protracted.

Genetic studies have also shown that Allen's Swamp Monkey is genetically conservative while several other species (notably de Brazza's Monkey and Hamlyn's Monkey) have long histories of genetic change. Both captive and wild guenons of different species hybridise easily. Early hybridisations between ancestors of living species offer one explanation for the complex genomic permutations of modern guenons. Guenons are therefore of great interest to geneticists, an interest that has been intensified by the implication of savanna monkeys in the epidemiology of AIDS.

GEOGRAPHY The fact that guenons are exclusively African is consistent with their relatively recent evolution and also their probable origination from a small, equatorial focus. Patas Monkeys and the savanna monkeys are secondarily adapted to arid conditions so that the basic characteristics of guenon biogeography can be represented diagrammatically as a series of concentric rings centred on the natal central African forests, but oscillating under the influence of climatic change. The most conservative forms, Allen's Swamp Monkey and the talapoins, are strictly equatorial, riverine species. By contrast their closest relative, the Patas Monkey, is likely to have been progressively displaced outward to the margins of habitable territory by more recently evolved species (notably the savanna monkeys).

Between these extremes, making up a complex mosaic, lie the other guenon species. Diana monkeys (whose ancestors were probably pioneers in colonising the forest canopy) survive in a few West African high forests. Mona and cephus monkeys, also arboreal, only occupy the main forest blocks while a larger, less exclusively arboreal group, the gentle monkeys, have been more successful in outlying peripheral forests with fewer competing species.

ECOLOGY Dividing guenons into mainly terrestrial and mainly arboreal groups obscures the more complex patterns of ecological adaptation that emerge if, for example, gait is related to foraging strategy. Thus, Allen's Swamp Monkey and talapoins can be described as versatile branch-walker/climbers restricted to dense cover. The much larger, so-called 'mountain monkeys', the *Allochrocebus* group, can climb but are mainly ground-foragers in fragmented forests with plenty of undergrowth. They probably had much more extensive ranges during glacial periods. Savanna monkeys are riverine ground-walker/climbers with a foraging strategy that demands fast, short-distance running. The Patas Monkey is a longer-distance loper-runner (and a marginal, yet still competent climber).

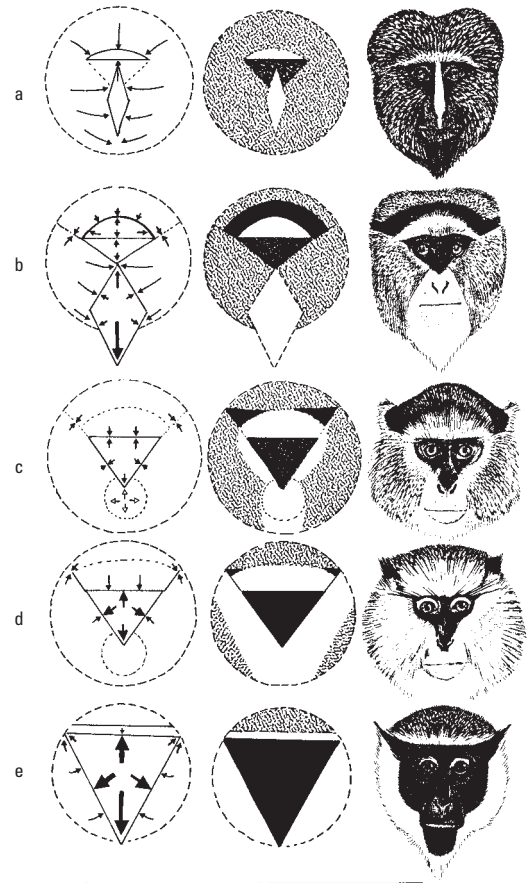
In the 'arboreal' division, de Brazza's Monkey is a slow-climber/walker restricted to relatively dense cover. The two diana monkeys are fast-climber/big branch-runners adapted to a relatively open canopy. Mona monkeys are fast-climber/small branch-runners. Cephus monkeys are fast, small branch-climbers and leapers while the larger, closely related gentle monkeys are versatile, wide-spectrum climbers and leapers. Owl-faced Monkeys are climber/walkers apparently combining gentle monkey and *Allochrocebus* foraging strategies with a special aptitude for slow, vertical climbing.

In addition to their different foraging techniques each guenon species has a different diet, which would seem to explain how multi-species communities of up to six species of guenons are able to live at high densities in most riverine or forest vegetation types.

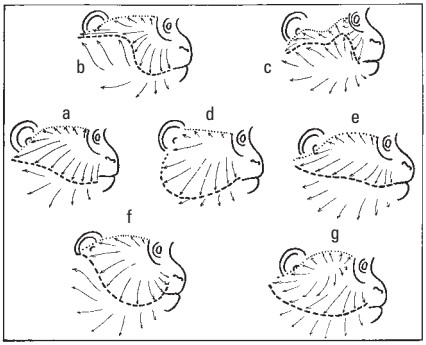
NATURAL HISTORY The success of guenons can partly be attributed to their species-specific foraging techniques, which reduce interspecies competition, and partly to their relatively egalitarian social systems, which place few constraints on females and young. Guenon territories are permanently occupied only by females while individual territorial males may come and go. The territorial male of a guenon group advertises and defends his tenancy of the territory and serves as its audio-visual marker. Females are not permanently dependent on him and they actively participate in defending the territory against other groups of females.

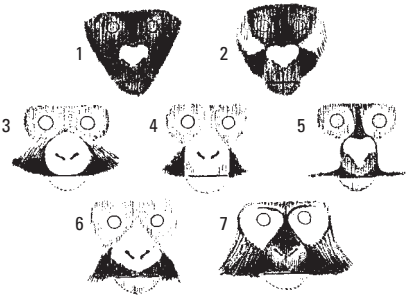
Guenons are very vocal and most have evolved species-specific loud calls. However, Allen's Swamp Monkey, the Patas Monkey and the talapoins appear to have retained many macaque-like vocalisations. Female guenons utter high-pitched bleats or barks which may serve to regulate distances between animals. Grunts help keep the group together, augmented by moans or quavers in some species. Warning calls consist variously of whistles, chirps and barks. Guenon calls are typically modulated and may identify the caller. In certain cases they also appear to identify a disturbance or predator as well as the status of the caller.

ADAPTATIONS In all guenon species the male is larger than the female and also more brightly coloured, but the differences are of degree not kind. The top diagram overleaf illustrates the underlying



Schematic diagram of tonal distribution on the faces of *Cercopithecus* species. (a) *C. hamlyni*. (b) *C. neglectus*. (c) *C.* (*mona*) *lowei*. (d) *C.* (*mona*) *campbelli*. (e) *C. diana*. C represents least differentiated pattern. Arrows on disks suggest intensifications of tonal contrast or extensions of tonal area.

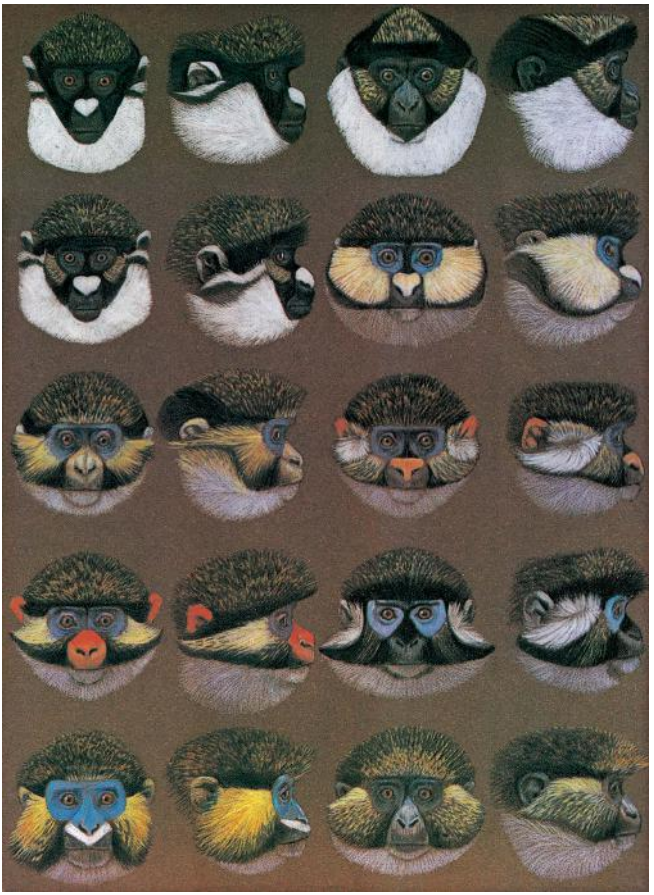




Below left and below: Cheek hair arrangement (*left* a–g) and tonal contrasts on facial masks (*right* 1–7) of *cephus* monkeys. Sclater's (b, 4), Lesser Spot-nose (*buttikoferi*, c, 2) (*petaurista*, 1), Moustached (d, 6), Red-eared (e, 3), Red-tailed (*schmidti*, f, 5), Red-tailed (*atrinasus*, g, 7), generalised guenon (a).

geometry of facial signals. Thus for species that rely on being cryptic, grizzled areas expand while in species that have developed facial signals an elaborate set of light and dark patches expands or contracts to generate an extraordinary diversity of signal patterns (see illustrations).

Guenons have evolved a range of specialised foraging strategies and tolerate continuous side-by-side foraging by other specialists. Such a situation risks losing the advantages conferred by dietary and other specialisations through wholesale hybridisation. Distinctive vocal repertoires, coat coloration and facial patterns appear to reduce the risk of excessive hybridisation between guenon species.



Face patterns in some *C.* (*cephus*) taxa.

Left: Lesser Spot-nose (*petaurista*)
Right: Nigerian White-throated (*erythrogaster*)

Left: Lesser Spot-nose (*buttikoferi*)
Right: Red-tailed (*schmidti*)

Left: Sclater's (*sclateri*)
Right: Red-tailed (*whitesidei*)

Left: Red-eared (*erythrotis*)
Right: Red-tailed (*atrinasus*)

Left: Moustached (*cephus*)
Right: Generalised guenon

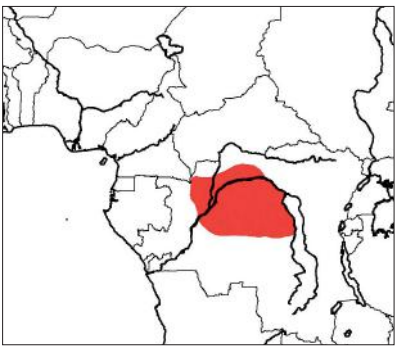
SWAMP MONKEY *Allenopithecus*

Genus with a single exclusively African species.

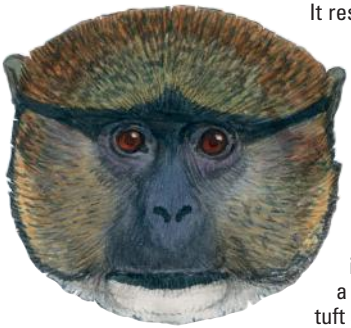
ALLEN'S SWAMP MONKEY

Allenopithecus nigroviridis

OTHER NAMES Fr. *Singe des marais, Cercopithèque noir et vert.* Ger. *Sumpf Meerkatze.*
MEASUREMENTS HB 330–410mm (♀), 450–510mm (♂). T 350–520mm. W 3.6kg (♀), 6.2kg (♂).
RECOGNITION Stocky khaki-coloured monkey with off-white underparts and a shortish tail that appears to be a survival of an archaic lineage in that it possesses anatomical features characteristic of macaques as well as guenons. Its intermediate status is confirmed by chromosome analysis. Allen's Swamp Monkey resembles guenons in the shape of its skull and in many details of its internal anatomy.



Allen's Swamp Monkey



Allen's Swamp Monkey, adult male

It resembles macaques or baboons in its gait, limb proportions, pointed ears, the loud rumbling calls and large testes of males and in the sexual swellings of females. The fur is soft and dense and especially long on the cheeks, where it forms a circular, grizzled facial disc. The darkened margins of this disc describe a sinuous curve over each cheek. Eyes are set deep beneath a broad, flattened cap. The muzzle is dark grey and the chin clear white. A strongly scented chest gland is marked by white bristles. First digits on the feet are long and powerful while the hand is shorter and broader than in any guenon. Adult males have a brilliant red margin to the anus above an orange perineal tuft and large, pale blue scrotum.

DISTRIBUTION Limited to the borders of the main Congo R. and its lower tributaries; also minor rivers and lake borders in the region and the borders of the R. Ubangi, R. Uelle, R. Kasai, R. Fini and R. Lukenyi. At the time when L. Congo existed, this monkey's predecessors were probably lake-shore dwellers.

HABITAT Swamp and levee forest bordering rivers and lakes. These forests are regularly and deeply flooded so that Allen's Swamp Monkey is arboreal during flood seasons and more terrestrial when water subsides. It makes forays into drier, more open habitats, including agricultural fields. Groups often sleep 8–20m above the ground in large trees close to or overhanging the river. Such sites are probably cool and safe and may serve to help space groups along a predominantly linear habitat.

FOOD Omnivorous. Forages in groups or subgroups of 4–57 individuals, taking fruits, leaves, stems, flowers, nectar and invertebrates (including earthworms and crabs). Seen to dive persistently and catch small fish manually.

BEHAVIOUR Small groups of 2–8 individuals feed together. Single males have also been recorded but they congregate with others in sleeping-trees, which suggests a harem, clan or band that can number more than 40 individuals. Group members utter short baboon-like grunts but also have a guenon-like, single, high-pitched warning chirp. Males make a rumbling or gobbling loud call.

ADAPTATIONS Male Allen's Swamp Monkeys have air sacs that serve to amplify their loud rumbling call. Similar calls uttered by some baboons, macaques and colobines suggest that this may have been a vocalisation common to many early African monkeys. A slightly sacculated stomach implies some capacity to digest difficult plant materials.

STATUS This monkey is easily hunted by torchlight from boats during the night and carcasses are frequently sold on the steamers and pirogues that ply the Congo R. In areas where cultivation borders the river, Allen's Swamp Monkey and its habitats are progressively constricted. The great extent and remoteness of much of its habitat makes any assessment of its status very difficult. IUCN lists as of least concern. Currently listed as Class B (African Convention), Appendix II (CITES).

TALAPOINS *Miopithecus*

Northern Talapoin	*Miopithecus ogouensis*
Southern Talapoin	*Miopithecus talapoin*

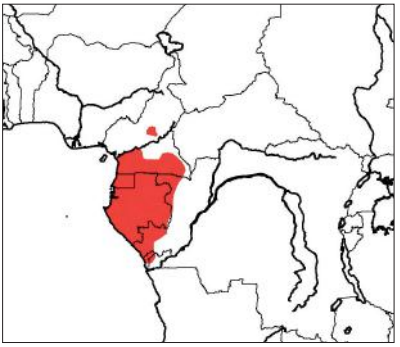
NORTHERN TALAPOIN

Miopithecus ogouensis

OTHER NAMES Gabon Talapoin Monkey. Fr. *Talapoin du nord*. Ger. *Ogoue Zwerg Meerkatze*.

MEASUREMENTS HB 230–340mm (♀), 260–360mm (♂). T 310–450mm. W 0.8–1.2kg (♀), 1.0–1.72kg (♂).

RECOGNITION A very small, large-headed monkey with a bright, grizzled yellow-olive crown and back, and golden-yellow outer surfaces to the limbs, hands and feet. The inner surfaces and underside are yellow tinged with off-white and the tail is dark-tipped. The naked skin of the face and ears is flesh-coloured with a yellowish tint to the eyelids and lips. There are darker streaks on the nose and on the margins of elaborate 'cow-licks' that sculpt the fur on cheeks and temples. Females have a pink sexual swelling. Males have a large, pale blue scrotum.



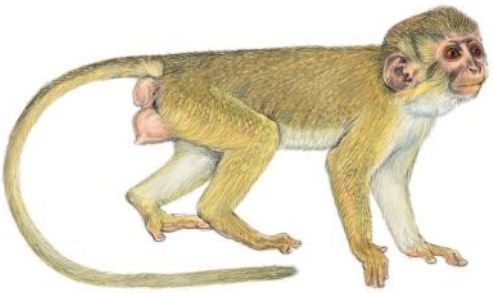
Northern Talapoin

DISTRIBUTION Equatorial coastal watersheds between Cabinda and the R. Nyong. The principal river and centre of its distribution is the R. Ogooué but its range spills over into the upper reaches of some Congo tributaries, such as the R. Sangha, R. Alima and R. Lefini.

HABITAT Strictly equatorial, riverine species never found more than 500m from a watercourse. The Northern Talapoin lives in the very dense undergrowth typical of riverbanks and seldom ascends to higher levels except through foliage-covered liane tangles. It can swim and dive under water if disturbed in overhanging vegetation. Terrestrial foraging is known to be common but it is rarely seen due to dense cover. Home ranges cover 100–500ha at densities of 40–90 animals per km^2.

FOOD In N Gabon, nearly 80% of the diet consists of fruits, notably those of plums (*Uapaca*), figs, umbrella tree (*Musanga*) and mokenjo (*Pseudospondias*), and the flesh of oil-palm nuts. Fruits of African ginger (*Aframomum*), gathered at ground level, are frequently eaten. Beetles, caterpillars and spiders are taken opportunistically. Riverside gardens of bananas, pawpaw, maize and cucurbits attract the Northern Talapoin out of the forest and manioc-washing sites are specially favoured for left-overs. Feeding is concentrated into one early morning bout, with another in late afternoon.

BEHAVIOUR Lives in groups of 12–20 that come together with other groups at specific night-roosts (situated in dense vegetation near water) numbering up to 115 animals. Adult males, less numerous than adult females, initiate movements and take up lookout posts, especially at night-roosts. Handling of captive females will precipitate attacks by males, suggesting that a defensive role for males is normal. Male threats are accompanied by head-bobbing, grimaces and lashing of the tail



tip. Outside the mating season males tend to move separately from the females (generally higher in the trees). In N Gabon all females tend to give birth annually between November and April. Females suckle their young for 4–5 months but young are very active and forage at an early age.

ADAPTATIONS The presence of a close relative, Allen's Swamp Monkey, with very similar habits, is probably the major factor explaining this talapoin's restricted range. Its dependence on dense evergreen cover is evidently due to its small size, which makes it potential prey to numerous carnivores, raptors and snakes. However, there must be special advantages in being a small monkey in an equatorial forest environment, as evident in the similar-sized squirrel monkeys of Amazonia.

STATUS It has been found that densities of the Northern Talapoin may double close to human settlements. Horticultural activity appears to offer at least three main benefits to these monkeys: predators are deterred by the human disturbance; clearing and land rotation generates secondary growth; and new food sources can be foraged in and around gardens. Human predation is discouraged by the talapoin's unrewarding size and its exceptional elusiveness. The Northern Talapoin is not threatened and has a low conservation priority.

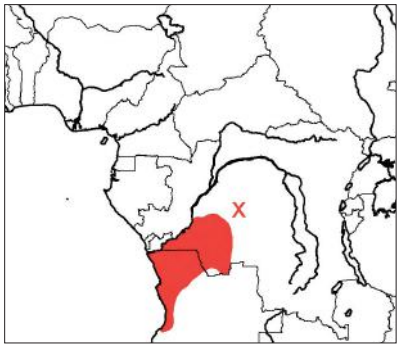
SOUTHERN TALAPOIN

Miopithecus talapoin

OTHER NAMES Angolan Talapoin Monkey. Fr. *Talapoin du sud*. Ger. *Angola Zwerg Meerkatze*.

MEASUREMENTS HB 320–400mm (♂). T 450–525mm. W (est.) 1–2kg.

RECOGNITION A small, grizzled, yellowish-olive monkey with pure white underparts and inner surfaces of limbs. The outer surfaces of the limbs are pallid chrome-yellow with less grizzling than the back. The white chin and cheek flash are separated by a black streak from the corner of the mouth. The bare skin of the face is black to the base of the nostrils, as are the ears. The tail is brown above and yellowish grey below. The legs are particularly long in relation to the arms and body. Females develop pink sexual swellings during oestrus. Males have a pale blue scrotum. They make louder calls than females and have longer canines.



Southern Talapoin

GEOGRAPHIC VARIATION *M. t. ansorgei*, *M. t. melahina*, *M. t. talapoin* and *M. t. vleeschouwersi* appear to be synonyms.

DISTRIBUTION Endemic to the coastal watersheds south of the Congo R., notably the R. Mebridege, R. Loge, R. Cuanza, R. Nhia and R. Cuvo (but spilling over into the upper reaches of the R. Cuango and now known from bank of R. Kasai).

HABITAT A strictly riverine species limited to dense evergreen vegetation on the banks of rivers that often flow through miombo (*Brachystegia*) woodland or, increasingly, cultivated areas.

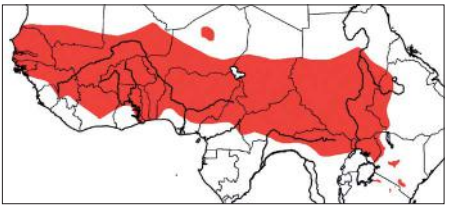
FOOD Mainly fruits but also seeds, young foliage and invertebrates.

BEHAVIOUR Southern Talapoins live in dense cover and so rely on sound more than visual markings in order to keep together. Their pigeon-like contact calls are almost continuous while they are moving or foraging. Home ranges are likely to be larger and densities lower than is the case with the equatorial species because forest strips are narrower and resources scarcer.
ADAPTATIONS Climatic fluctuations have probably reinforced the Southern Talapoin's primary adaptation to 'strip-living'. Longer dry seasons and less extensive flooding under generally cooler and drier climates may have favoured more terrestrial habits than are apparent in the Northern species. Consistent with such differences are the Southern Talapoin's longer limbs and larger body size.
STATUS Very little is known about this species and still less about its current status. It may not be threatened yet and currently has a low conservation priority rating but land-use practices are changing.

PATAS MONKEY *Erythrocebus*

Genus with a single exclusively African species.

PATAS MONKEY *Erythrocebus patas*



Patas Monkey

OTHER NAMES Hussar Monkey, Nisnas. Fr. *Patas, Singe rouge*. Ger. *Husarenaffe*.
MEASUREMENTS HB 490–720mm (♀), 600–750mm (♂). T 430–740mm. W 5.4–8kg (♀), 10–18kg (♂).
RECOGNITION A highly distinctive monkey with long limbs and slender build. Females and young are the colour of dry grass, with shades of fawn, russet and grey. Males are larger and have russet tails, hindquarters and crowns. The back and nape are sandy coloured and the shoulders are shaggy and grey-streaked. Limbs are white or off-white. Western populations have pale facial skin and a dark nose; those in the east have black facial skin and a white nose. The scrotum and its surrounding skin are blue. The penis is pink and the anus of the male is surrounded by bare violet-pink skin.
GEOGRAPHIC VARIATION *E. p. patas* (main Sahel population from Mauritania to Kordofan), *E. p. pyrrhonotus* (main Nile Valley population from South Sudan to Uelle and Kenya).

Two very small isolated populations have been treated by some authorities as subspecies, namely *E. p. villiersi* (Aïr massif isolate) and *E. p. baumstarki* (pallid Serengeti isolate).
HABITAT Vegetation types ranging from open grassland to dry woodland; commonest in thinly bushed acacia-wooded grassland. On floodplains, Patas Monkeys prefer to travel along the edges

of wooded levees, moving from tree to tree with frequent stops to monitor their surroundings. All classes are vigilant but adult males are especially so. The area travelled by a Patas troop varies with the season, topography and food resources of the range (about 20–30km^2 in richer habitats and up to 80km^2 in poorer ones). Densities may decline from a known optimum of about 1.5 per km^2. A group may travel up to 12km in a day.

FOOD Especially dependent on the pods, seeds, galls, young leaves, gum and flowers of *Acacia*, especially *A. drepanolobium*, and the fruits of common savanna trees and shrubs, such as torchwood (*Balanites*), *Euclea* and num-num (*Carissa*). Patas Monkeys are poor diggers and only take grass rhizomes and leaf bases when these are in crumbly soil. Insects, small vertebrates and fungi are also taken. Visits to water are frequent in the dry season and are occasions for great vigilance.

BEHAVIOUR Maintain single male, multi-female groups but size of group may fluctuate. All members of a group tend to forage in well-spaced scatter. Group ranges vary in degrees of overlap with neighbours but some may share over 58% of range. Nonetheless groups are mutually intolerant. Males often stay some distance from the main troop but are aggressive towards other males in the presence of females. Weakly defined pecking orders have been observed among females. Solitary males and small bachelor groups have also been recorded. Patas Monkeys are relatively quiet monkeys and males do not make loud calls. A low moan or moo is the characteristic contact call. Females and young have a repertoire of chirrups, twitters, hoots and low whistles. Cohesion and precise communication are particularly important for small groups living in open, and consequently dangerous, environments.

Females in oestrus do not have obvious sexual swellings but advertise their condition through their gait, by puffing up their cheeks, pursing their lips and by uttering a 'want' moan. Gestation lasts about 24 weeks and there tend to be pronounced mating peaks marked by an influx of males into former one-male groups (July–August in Kenya). Births are seasonal but variable. New babies are dark brown and females are intensely possessive of their young. Females become mature at 3.5 years. Full development may be delayed in some males but is reached by 5 years of age. Life expectancy in the wild is about 17 years but a captive has been recorded as living 24 years.

ADAPTATIONS The long limbs of Patas Monkeys equip them for fast movement. Their hands and feet are narrow and the heel is long. The toes and fingers are short and have relatively weak grasping power. Patas Monkeys probably descend from monkeys that adapted to the driest northern margins of the Congo basin, from whence they are likely to have been further displaced by early savanna monkeys. The large size of males relative to females could be a relatively recent, secondary development.

STATUS Recent changes throughout their range have affected Patas Monkeys. In particular they have disappeared from areas in which trees have been cleared and in which cultivation and hunting have intensified. On the other hand, they have readily adapted to feeding on exotic foods, from prickly pears and *Lantana* to cotton plants and food crops. Furthermore, elimination of wild predators has probably favoured them in some localities. Patas Monkeys have been declared vermin by several African countries and they are used as laboratory animals.

SAVANNA MONKEYS *Chlorocebus* group

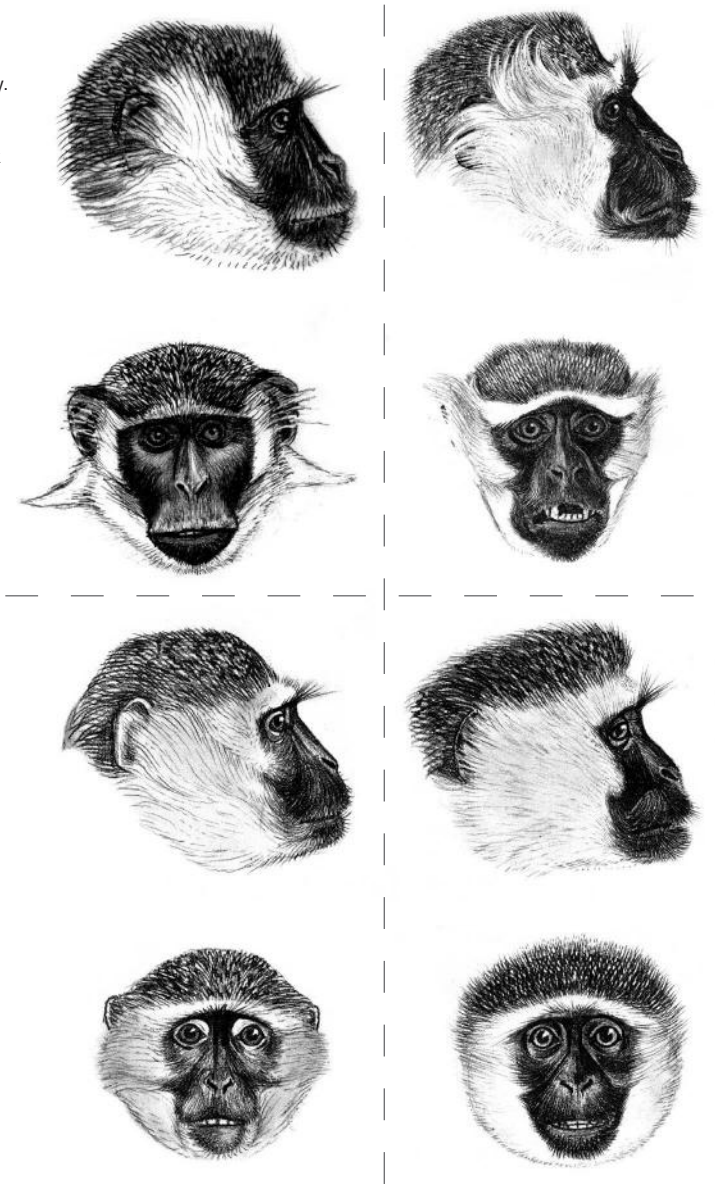
OTHER NAMES Fr. *Grivet, Singe vert*. Ger. *Grunmeerkatze*. Swah. *Tumbili, Ngedere*.

RECOGNITION Small, grizzled, grey, brownish or greenish monkeys with a black face mask, white ruff and a pale (or white) underside. The tail is long (except in the montane Bale Monkey). There are stiff black bristles on the brow ridge in all species. The scrotum is blue or bluish in all species and both sexes have blue belly skin showing through thin white hair. The penis is red or pink and females in oestrus have a bluish vulva and a pink clitoris.

GEOGRAPHIC VARIATION Grivet Monkey, *C. (a.) aethiops* (Sudan and Ethiopia); Bale Monkey (Djam-Djam Monkey), *C. (a.) djamdjamensis* (Bale massif, Ethiopia); Tantalus Monkey, *C. (a.) tantalus* (northern savannas from Ghana to Uganda); Vervet and Malbrouk Monkeys, *C. (a.) pygerythrus* (southern savannas and woodlands from Cape of Good Hope and Angola to Somalia); Green Monkey, *C. (a.) sabaeus* (northern savannas from Ghana to Senegal). Because all forms are mutually fertile and hybridise along range boundaries, savanna monkeys are sometimes treated as a single species.

DISTRIBUTION By far the most numerous and widespread monkeys in Africa, ranging throughout the non-desert, non-forest areas of the continent and formerly extending along the Nile Valley.

HABITAT Savannas, woodlands and forest–grassland mosaics. Savanna monkeys typically live along the thin but continuous belts of vegetation that follow drainage lines. Trees along these



Four savanna monkey *Chlorocebus* species (adult males).
Top left: Green Monkey.
Top right: Tantalus Monkey.
Bottom left: Malbrouck Monkey.
Bottom right: Vervet Monkey.

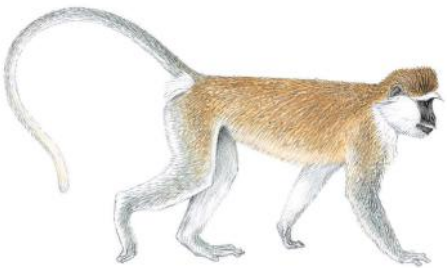
narrow belts are often deciduous. Savanna monkeys therefore forage on the ground for part of the year, usually at some distance from the trees on which they depend for shelter, shade and much of their food supply. The distribution pattern of these monkeys is therefore strongly linear, following tree/grassland edges all over their wide range.

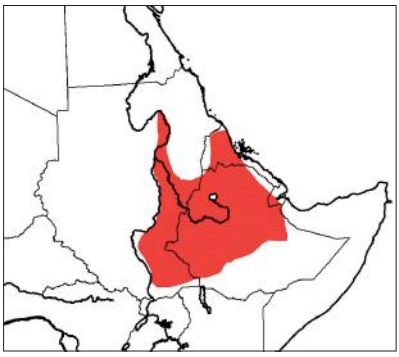
The extent of a group's home-range varies from 13ha to 178ha, according to habitat, food resources and the influence of neighbouring groups. In rich environments large groups can defend small, exclusive territories. In poor habitats small groups disperse over large, undefendable ranges and population densities are consequently much lower.

FOOD Fruits are the preferred and most important food, flowers and seeds become important outside fruiting seasons, and foliage and animal foods can be significant in some areas and during certain seasons. Seeds, flowers, leaves and gum of *Acacia* are important wherever this tree is dominant. The exceptionally small thumb, characteristic of these monkeys, may help to explain why they are rather inept at catching and handling active insects.
BEHAVIOUR Savanna monkey groups may number 5–76 animals (mean 25). Both females and males follow a rank hierarchy but female coalitions modify the pecking order and deter male aggression towards the young. All young males leave their natal group (usually joining their nearest neighbours) whereas females habitually remain with their maternal group. Males only concert their actions during confrontations with other groups. During group challenges males make ritualised standing 'red, white and blue' displays with erect penises. During encounters between neighbouring groups females tend to be less aggressive. Birth timing is subject to much regional variation. Young mature fast and females can conceive at less than 2 years of age; males are fertile by 3 years. Mature weights and development reached at 4 years for females and 5 years for males.
ADAPTATIONS Equally at home in trees and on the ground. Can withstand sustained solar radiation, high temperatures and dehydration. Have adapted to extreme climatic instability with high birth rates during good periods: fertility and activity are reduced during droughts and famines. Adjust to changes in environment, such as the opening up of forest or woodland areas as a result of road-making, logging, cultivation, elephant damage, flooding etc. Their alertness and acute vision is only exceeded by the Patas Monkey, which they resemble in that high-ranking males are the most continuously vigilant members of the group. High fecundity not only allows rapid response to huge fluctuations in food supply but also offsets heavy predation by eagles, pythons, Leopards and other carnivores.
STATUS With the single exception of the Bale Monkey, all populations of savanna monkeys are still abundant, although the northern limits of their distribution are contracting as a result of tree-clearance in the Sahel. Savanna monkeys were extensively used for medical research until the deaths of several laboratory workers from Marburg virus (transmitted by Vervet Monkeys) deterred what had been a substantial trade. Their natural immunity to SIV (very close to the human AIDS virus, HIV) has prompted continued interest in their biology.

GRIVET MONKEY *Chlorocebus aethiops*

OTHER NAMES Fr. *Grivet d'Ethiopie*. Ger. *Aethiopen Grummeerkatze*.
MEASUREMENTS HB (est.) 400–600mm. T (est.) 420–700mm. W (est.) 5–8kg.
RECOGNITION A long-tailed savanna monkey with variable, warm-olive grizzled back and crown, grey limbs and a white underside. The prominent cheek-fur is laterally elongated and there is a narrow white band above the brows. The face is black (often with a fine white moustache), hands and feet are pale and there is a white tuft at the base of the white-tipped tail. In males the scrotum is sky blue.
GEOGRAPHIC VARIATION *C. a. aethiops* (east of R. Nile from Sudd to Eritrea). *C. a. matschei* (montane Ethiopia west of the Rift Valley): variable fawn to russet back. Possibly hybridised with Bale Monkey west of the Rift Valley, as the latter's forest habitats were destroyed over the last two millennia.
HABITAT Savannas, woodlands, riverine strips and cultivation mosaics.
FOOD Heavily dependent on acacia seeds, flowers, foliage and gum. Also figs and other fruiting trees.



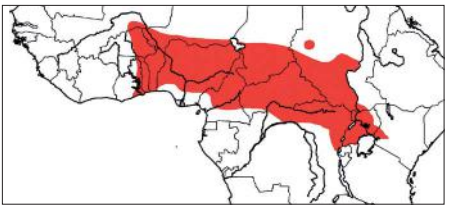


Grivet Monkey

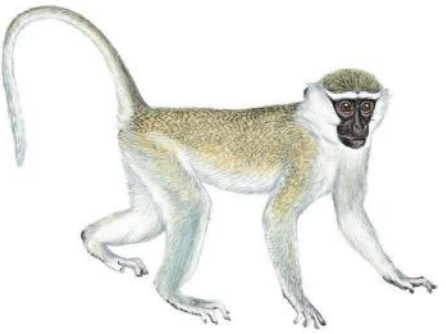
TANTALUS MONKEY

Chlorocebus tantalus

OTHER NAMES Fr. *Cercopithèque tantale*. Ger. *Tantalusmeerkatze*. Swah. *Tumbili, Ngedere*.
MEASUREMENTS HB 380–830mm. T 550–1,140mm. W (est.) 3–9kg.
RECOGNITION The largest of the savanna monkeys, with grizzled, gold to greenish back and crown, grey limbs and a white underside. The long tail has a pale tip and a white tuft at base. The face and temple bar are black and there is a sinuous, tapered white brow-band. In males the scrotum is sky blue.
GEOGRAPHIC VARIATION *C. t. tantalus* (Ghana to R. Ubangi): olive-green back. *C. t. budgetti* (R. Ubangi to Uganda and South Sudan but with broad hybrid zone around shores of L. Victoria): olive-brown back. *C. t. marrensis* (isolate on desert mountain massif of Jebel Marra): light olive-fawn back.
HABITAT Woodlands, savannas and forest mosaics.
FOOD Fruits, buds, seeds, roots, bark, gum and many cultivated plants. Insects, small vertebrates and eggs are also taken.



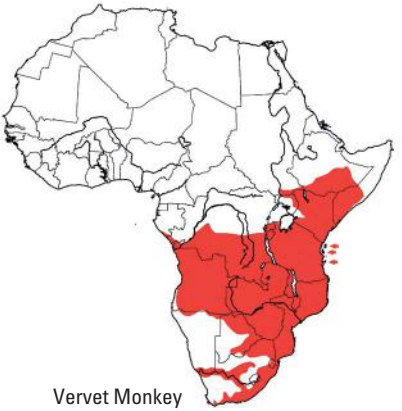
Tantalus Monkey



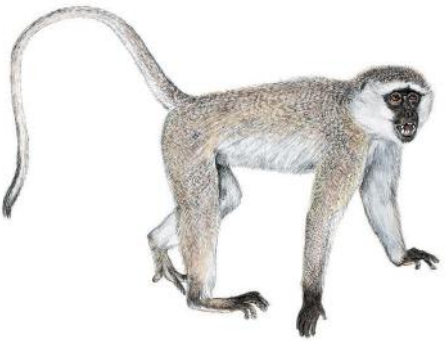
VERVET MONKEY

Chlorocebus pygerythrus

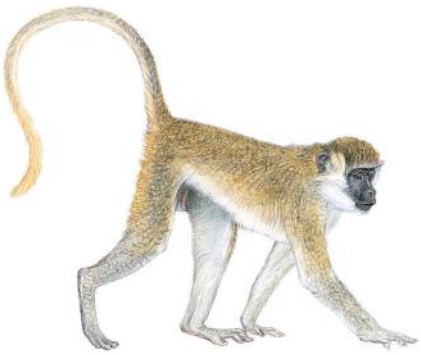
OTHER NAMES Fr. *Vervet*. Ger. *Sudafrika Grunmeerkatze*. Swah. *Tumbili, Ngedere*.
MEASUREMENTS HB 420–510mm (♀), 430–570mm (♂). T 480–750mm. W 3.4–5.3kg (♀), 4–8kg (♂).
RECOGNITION A long-tailed monkey with a grizzled, grey or olive back, crown and outer limb fur. Hands and feet are darker and there is a dark tip to the tail. Tufts at the base of the tail are red. The white brow and cheeks join to frame the black face. The scrotum is turquoise or lapis blue.
GEOGRAPHIC VARIATION *C. p. pygerythrus* (eastern–southern Africa south of R. Zambezi): ash-grey coat in west graduating to olive-green. *C. p. rufoviridis* (Indian Ocean to Rift lakes between R. Zambezi and L. Victoria): olive-fawn back. *C. p. arenarius* (Somali arid zone from Horn of Africa to E Uganda and N Tanzania): brownish back and generally pallid colouring; hybridises with *C. tantalus* along northern shores of L. Victoria and possibly with *C. djamdjamensis* in SE Ethiopia. Dwarf forms are found on Indian Ocean islands and islands in L. Victoria, i.e. *excubitor* (Patta I.) and *nesiotes* (Pemba I.). *C. p. cynosurus*, Malbrouck Monkey (sometimes treated as a

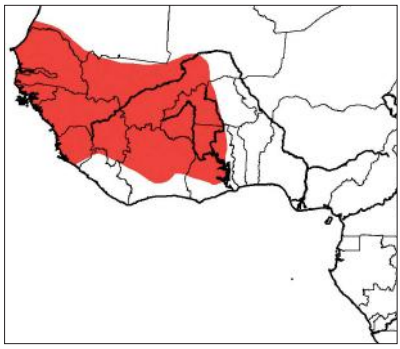


Vervet Monkey



separate species) (Atlantic to Rift Lakes south of rainforests): olive-grey with pale-blotched face, lapis scrotum and cow-lick on cheeks in the north-west.
HABITAT A wide variety of lightly wooded habitats across some 45 degrees of latitude, straddling the Equator, ranging over half the continent and reaching altitudes of up to 3,000m. A significant part of the total range consists of miombo (*Brachystegia*) fire-climax woodlands. Although Vervets may range through these and other woodlands during fruiting or flowering seasons, acacia-dominated riverine strips are primary habitat.
FOOD Especially important are the seeds, flowers, foliage and gum of *Acacia* and *Albizia*, as well as the fruits of figs and buffalo thorn (*Ziziphus*). During the fruiting seasons of marula (*Sclerocarya*) or raisin bush (*Grewia*), Vervets may disperse into wider fruiting zones. Animal foods are of minor significance in most habitats but may play a larger role in mangrove swamps of the east coast and islands.





Green Monkey

GREEN MONKEY *Chlorocebus sabaeus*

OTHER NAMES Callithrix Monkey. Fr. *Singe vert*. Ger. *Grunmeerkatze*.
MEASUREMENTS HB 420–460mm. T (est.) 420–720mm. W 3.4–5.9kg (♀), 4.7–7.5kg (♂).
RECOGNITION Long-legged savanna monkey with grizzled golden-green extending over the back, crown, down the upper arms, thighs and base of the tail. Hands and feet pale grey, underside off-white. Tip of tail pale orange. Yellowish cheek-ruffs are deflected by a cow-lick which begins below the prominent black ears and sweeps up over the temples. There is barely a trace of light brow-band. The scrotum is very pale blue.
HABITAT A wide range of ecotypes, including very dry Sahelian woodlands, rainforest margins and mangrove swamps.
FOOD The diets, survival and social structure of the mangrove-dwelling Green Monkey have been extensively studied. One of its peculiarities is a reliance on crabs and other seashore foods, which are taken on mudflats at low tide.
STATUS In Senegal this species is the subject of important research on the epidemiology of SIV. Evidence of infection with this virus has been found in 46% of a wild population of Green Monkeys while only 6% of Patas Monkeys in the region showed evidence of infection (differences probably connected with differing socio-sexual behaviour). Green Monkeys are naturally immune to diverse strains of AIDS-like viruses. Research is focused on a strain that might also be harmless to humans while at the same time providing immunity against HIV.

BALE MONKEY *Chlorocebus djamdjamensis*

OTHER NAMES Djam-Djam Monkey. Fr. *Cercopithèque de Bale*. Ger. *Bale Grunmeerkatze*.
MEASUREMENTS HB 430–450mm. T 470–500mm. W 3.0–3.6kg (♀).
RECOGNITION A relatively short-tailed monkey with thick, long fur. The back and crown are variably grizzled deep brown to yellowish brown, limbs and tail are grey and extremities are dark grey. The underside is off-white to grey. The black face, brows and temples show no trace of white except for a fine white moustache. The short white chin and cheek-ruff leave the ears exposed and there are inconspicuous red-brown tufts at the base of the tail. Males have a blue scrotum.

Bale Monkey

Bale Monkey

GEOGRAPHIC VARIATION Numerous races of savanna monkey have been described for Ethiopia, the meeting point for three distinct species: *aethiops*, *pygerythrus* and *djamdjamensis*. Many of these might represent various permutations of hybrid, e.g. *hilgerti*, *ellenbecki*, *matschiei* and *zavattarii*, some of which might possibly include traces of *C. djamdjamensis* genes.

Probably the Bale Monkey was originally distributed over all regions of the Ethiopian massif where bamboo forests grew. Clearance over more than 2,000 years has probably favoured the upward spread of Grivets from the lowlands. In any event, typical Bale Monkeys are now restricted to small and remote areas of bamboo forest in SE Ethiopia.

Because this population is so distinctive it seems likely that it has become the specialist relict of an older regional population belonging to the very earliest dispersal of savanna monkeys.

HABITAT So far the Bale Monkey has been recorded only from the bamboo zone and it seems unlikely that the adoption of this diet is a new development. Such extreme specialisation suggests that primate niches within Ethiopian mountain forests were thoroughly and densely partitioned out before human settlement. Extant colobus monkeys, gentle monkeys and baboons would represent obvious candidates but previous presence of now extinct primates is also a possibility.

FOOD In one study young bamboo leaves and pith accounted for 77% of diet, *Dombea torrida* and *Psychotria orohila* were other important sources of leaves and flowers. Animal foods were minimal.

STATUS Further study of this unique monkey, especially its digestive physiology, should be a priority, particularly in view of its much diminished range. It occurs in a small part of the proposed Bale NP and it is urgent that confirmation of the status of this park is enacted. The Bale Monkey inhabits a region of great biogeographic importance where many other unique species of fauna and flora are similarly endangered. IUCN rates it as vulnerable.

Bale Monkey

MOUNTAIN MONKEYS *Allochrocebus* group

OTHER NAMES Fr. *Cercopithèques de montagne*. Ger. *Vollbart Meerkatze*.
RECOGNITION Long-limbed dark monkeys living on forest floor. Black muzzle stands out in sharp relief against a white ruff around the chin. Male mountain monkeys vie with Patas Monkey males in being the largest, longest-muzzled guenons, and in their shared high degree of sexual dimorphism. Typical display postures adopted during male–male or group encounters are illustrated on pp.140 and 155, showing tail raised and tip curled into a question-mark shape. Rapid about-turns also display the brilliant blue scrotum against its background of black fur. The contrast between low-key colours and behaviour on the one hand, and striking intra-specific visual display on the other, is typical of mountain monkeys, which are usually silent animals.

L'Hoest's Monkey

Preuss's Monkey adult male

Sun-tailed Monkey

GEOGRAPHIC VARIATION L'Hoest's Monkey, *A. lhoesti* (highland and lowland forests in E DR Congo, Uganda, Rwanda and Burundi). Preuss's Monkey, *A. preussi* (highland and lowland forests in SW Cameroon and SE Nigeria). Sun-tailed Monkey, *A. solatus* (evergreen forest in central Gabon). It has been suggested that the terrestrial long-faced monkeys, *C. (hamlyni)*, which resemble *Allochrocebus* in several respects, might be related and ancient hybridisation remains a possibility. However, most genetic studies are unequivocal in placing *C. (hamlyni)* in *Cercopithecus*, making the resemblances a striking instance of convergence.
DISTRIBUTION Distribution of the three mountain monkey species are probably best understood in relation to past glacial conditions that are best preserved at higher altitudes ('mountain' is a misleading name in this respect). The foraging environments common to all three species consist of disturbed areas such as old landslides, tree-fall chablis and flood-scoured valleys where a major resource is ground herbs and vegetation that is continuously re-sprouting.

These monkeys live in small, tight-knit groups in well-defined home-ranges and are demonstrably poor dispersers. Perhaps a dependence on continuity of group experience might make it difficult for them to regain ground lost to cultivation.
HABITAT Lives on the forest floor, usually on broken ground or steep slopes. Large ranges suggest that feeding strategies are expansive rather than intensive. Indeed groups of these monkeys have been observed to travel between dense mountain retreats and more exposed feeding sites down 600m of rugged escarpment, sometimes making the descent and returning twice in a single day. The fact that these monkeys regularly visit particular feeding sites during the appropriate season and are frequently seen at the same crossing points suggests that they possess intimate knowledge of their home ranges. Known to prefer a combination of rough, steep slopes and dark, dense cover, intimate knowledge of home ranges of this kind probably allows these highly mobile monkeys to stand up to competition from other species and to elude predators.
FOOD Mainly fruits and seeds; shoots, young leaves, buds, flowers and mushrooms. Mountain monkeys feed in close formation and are not known to feed from scarce, scattered sources that would force a group to disperse in order to harvest them. When cultivation expands into their home-ranges they invariably become wary but persistent raiders, invading agricultural fields in tight groups. Only occasionally join other species in mixed feeding groups, probably drawn by particularly plentiful food sources.
BEHAVIOUR A single adult male with one or more females and their offspring form the usual social unit of up to 10 individuals. Home-ranges are probably too large to defend but confrontations

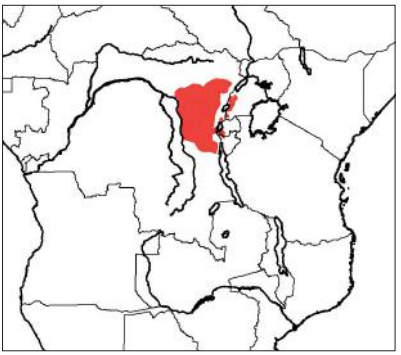
between groups involve all members. Adult males make frequent threats and rushes, and posture with tail raised and chin thrust forward, frequently turning to display frontal, lateral and back views. This is usually followed by a silent and sudden withdrawal.

ADAPTATIONS These species are remarkable for their ability to run through dense undergrowth. Their limbs show minor modifications that render the relatively unspecialised hands and feet particularly flexible at the wrist and ankle. Exceptional wariness and quietness evidently help to reduce predation (by Leopards, African Golden Cats, pythons and eagles) but low-key forms of communication mean that individuals can easily get lost and so must stay close together. A poor ability to disperse probably inhibits the colonisation or re-colonisation of territory and gives rise to a patchy distribution at both micro- and macro-level.

The original divergence between mountain monkeys and savanna monkeys was likely to have been influenced by frequent and repetitive oscillations in climate during which L'Hoest's Monkeys adapted to wetter and savanna monkeys to drier conditions.

STATUS These monkeys respond to agricultural encroachment by raiding crops and are therefore frequently snared and hunted. Because their social and foraging habits depend on continuity and stability, any major perturbation is likely to lead to decline. This may be one of the few primate groups in which captive-breeding programmes might contribute to their survival. In the future they might be expected to respond well to carefully phased re-introduction to well-protected, florally rich areas.

L'HOEST'S MONKEY *Allochrocebus lhoesti*

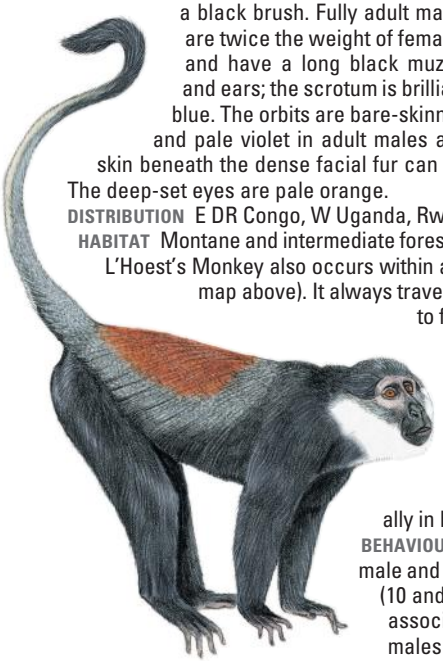


L'Hoest's Monkey

OTHER NAMES Fr. *Cercopithèque de l'Hoest*. Ger. *Vollbartmeerkatze*.

MEASUREMENTS HB 420–600mm (♀), 510–700mm (♂). T 460–800mm. SH (est.) 290–360mm (♀), 340–460mm (♂). W 1.6–5.2kg (♀), 3.2–8.5kg (♂).

RECOGNITION A long-legged, black-bodied monkey with a brilliant white ruff and a russet 'saddle' bordered with grizzled bluish grey. The long tail is grey at its thick base and tapers to a black brush. Fully adult males are twice the weight of females and have a long black muzzle and ears; the scrotum is brilliant blue. The orbits are bare-skinned and pale violet in adult males and skin beneath the dense facial fur can be brilliant blue, pink or purple, pale or jet black. The deep-set eyes are pale orange.



DISTRIBUTION E DR Congo, W Uganda, Rwanda and Burundi.

HABITAT Montane and intermediate forest up to 2,500m from Itombwe to the Ruwenzori Mts. L'Hoest's Monkey also occurs within a wedge of lowland forest west of this region (see map above). It always travels on the ground but will climb to any level in order to feed.

FOOD Young leaves and shoots of various trees, shrubs, grasses and herbs, fruits of yellowwood (*Podocarpus*), koso (*Hagenia*), parasol trees (*Polyscias*), wild custard apple (*Myrianthus*), wild poplar, *Macaranga*, *Maesa*, resins, bracken shoots and mushrooms, invertebrates and lichen are eaten opportunistically, occasionally in bulk and more in the dry season.

BEHAVIOUR L'Hoest's Monkey groups consist of a single male and a very variable number of females and their young (10 and 17 are two cited averages). Groups form a close association reinforced by much mutual grooming. Adult males tend to stay on the periphery and take up the rear

when the group is alarmed. Solitary males are frequently found in the vicinity of larger groups. A group will usually use one of a limited number of favourite sleeping-trees (usually situated in higher locations) at night. Newborn infants are brown and acquire adult colours over the first 2–3 months. They are frequently observed to entwine tails with their mother.

ADAPTATIONS The long legs of this species correlate with its frequent and extensive travel within large home-ranges. While many other guenon species elude predators by hiding in the trees, L'Hoest's Monkey flees over the ground, a strategy that requires thorough knowledge of the range and coordination among all members in order to keep together as a group.

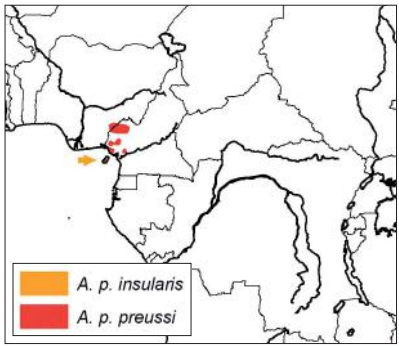
STATUS Erosion of habitats as a result of expanding cultivation, together with concomitant hunting, are probably reducing L'Hoest's Monkey numbers in many areas. While light selective felling and pit-sawing probably favour this species, large-scale logging is known to have threatened it in Kibale Forest, Uganda. The monkey's last stronghold in Rwanda, the Nyungwe Forest, is threatened by a major Development Action Plan. Although its wide range and diverse habitats ensure the immediate future of this species, long-term prospects are less secure. Listed as Class B (African Convention), Appendix II (CITES), vulnerable (IUCN).

PREUSS'S MONKEY *Allochrocebus preussi*

OTHER NAMES Fr. *Cercopithèque de Preuss*.
Ger. *Westafrika Vollbart Meerkatze*.

MEASUREMENTS HB 450–530mm (♀) 550–605mm (♂) T 490–690mm. W (est.) 3.5–7kg.

RECOGNITION A long-tailed, long-legged dark monkey with grizzled grey crown, cheeks, shoulder and flanks. A mahogany-red streak extends from the shoulders to the root of the tail. The vivid orange eyes are set in pale violet orbits. The muzzle, nose and forehead are black and there is a furry white bib. The adult male has a blue scrotum, a long, prominent muzzle and is twice the weight of the female.



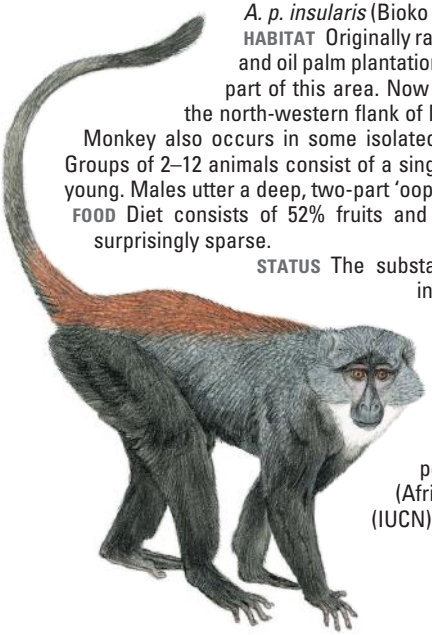
Preuss's Monkey

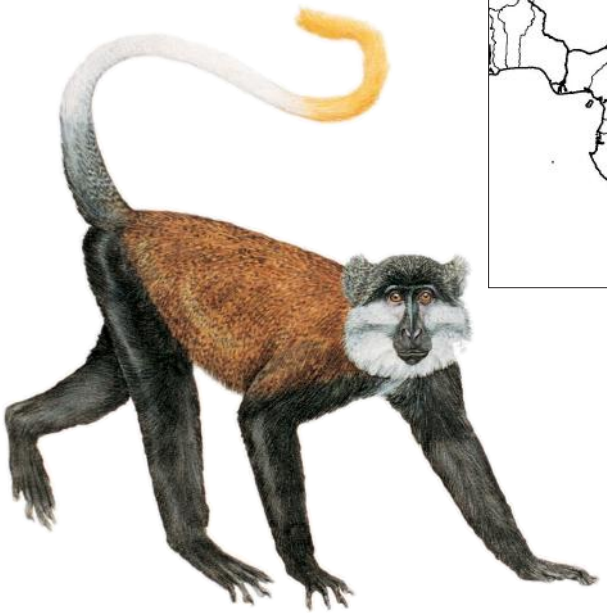
GEOGRAPHIC VARIATION
A. p. insularis (Bioko I.), *A. p. preussi* (mainland).

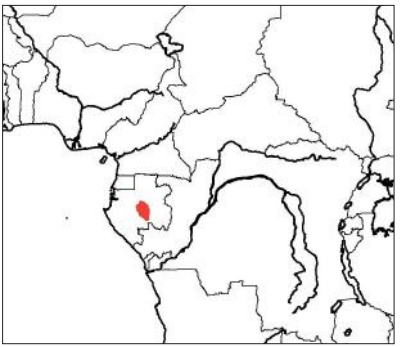
HABITAT Originally ranging from the R. Sanaga to the Cross R. but rubber and oil palm plantations have exterminated this species over the greater part of this area. Now found in the Oban hills and Obudu but mainly on the north-western flank of Mt Cameroon between 1,000 and 1,800m. Preuss's Monkey also occurs in some isolated patches of forest in the Cameroon grasslands. Groups of 2–12 animals consist of a single adult male and one or more females with their young. Males utter a deep, two-part 'oop-uuh' in the morning and early evening.

FOOD Diet consists of 52% fruits and over 40% other plant parts, with animal foods surprisingly sparse.

STATUS The substantial contraction of this monkey's range is an indication of how profoundly Cameroon forests have suffered from clear-felling (for chipboard and plantations), cultivation, hunting and the penetration of forests by roads and settlement. Confiscation of guns in Bioko in 1976 brought temporary respite but uncontrolled bushmeat hunting continues. The distribution of both populations is extremely confined. Listed as Class B (African Convention), Appendix II (CITES), endangered (IUCN).







Sun-tailed Monkey

SUN-TAILED MONKEY *Allochrocebus solatus*

OTHER NAMES Fr. *Cercopithèque à queue de soleil.* Ger. *Sonnenschwanzmeerkatze.* Sake dialect *Kage*.

MEASUREMENTS HB 450–540mm (♀), 460–580mm (♂). T 560–760mm. W 3.7–4.3kg (♀), 5.8–8.7kg (♂).

RECOGNITION Limbs are long and black, the back is grizzled brown and the grey and white tail is tipped with bright orange. The crown is grizzled grey with prominent muffs over the ears. Pale grey cheek patches are poorly differentiated from a circular off-white bib. Males are much larger than females and have a bright blue scrotum and a prominent muzzle.

DISTRIBUTION Central Gabon between the valleys of the R. Ogooué and R. Offoué (but scarcely any records east of the R. Ogooué).

HABITAT A hilly area of approximately 10,000km^2 typified by very frequent rivers and streams that dissect the terrain deeply. The moist evergreen forest is dominated by Gaboon mahogany (*Acoumea*), the leguminous awoura (*Julbernardia*), false nutmeg (*Pycnanthus*) and mubala-oil trees (*Pentaclethra*). The Sun-tailed Monkey prefers densely shaded, tangled areas and remains common after light logging (probably because dense undergrowth increases).

FOOD Fruits and seeds 26% in one study, 27.5% invertebrates. The balance was made up of mushrooms and various plant parts.

BEHAVIOUR Small single-male, multi-female groups. The forest in the Sun-tailed Monkey's area is inhabited by 13 other species of simian primate. This is a measure of the abundant food resources available but also suggests it is currently not in direct competition with other species.

STATUS First described as late as 1988, the Sun-tailed Monkey has become a 'flagship' species for conservation in Gabon. Its limited distribution is not due to hunting, settlement or logging, although logging concessions are being exploited over most of its range in the Forêt des Abeilles. Given the importance of this area for very many organisms, the proposed Lopé NP should be enlarged to include the Forêt des Abeilles as a unique centre of endemism, or refugium. Listed as Class B (African Convention), Appendix II (CITES), rated by IUCN as vulnerable to extinction.

ARBOREAL GUENONS *Cercopithecus*

Genus of 21 exclusively African species (listed under Cercopithecini).

DRYAD MONKEYS *Cercopithecus (dryas)* group

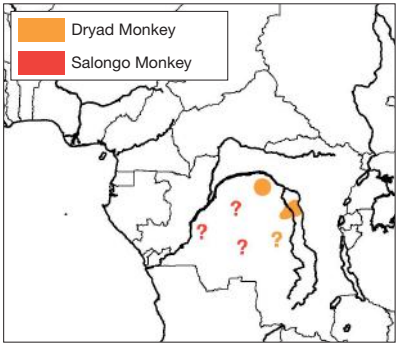
This problematic taxon was presented in the first edition of this guide as a single, rare and secretive species, its appearance deduced from the skins and photos available in 1994. Since then variously coloured pelages have been described for which two names (*dryas* and *salongo*) are used.

Differences might be regional (i.e. populations brighter in the eastern Congo basin, paler in the west?), might signify species, subspecies, cline or polymorphs, or be influenced by age, sex or hormones.

Two pelage types and given names (still provisional and tentative) are presented here to encourage more research. Attempts to differentiate habitats or habits are currently premature.

DRYAD MONKEY

Cercopithecus (dryas) dryas



Dryad and Salongo Monkeys

OTHER NAMES Inoko Dryad Monkey. Fr. *Cercopithèque Inoko*. Ger. *Inokomeerkatze*.

MEASUREMENTS (both forms of *dryas*) HB (est.) 365–400mm. T (est.) 480–520mm. W (est.) 2.0–3.3kg.

RECOGNITION In 1932 *C. dryas* was named from a skin reportedly taken from the Tumbenga Valley (near Lomela, W of R. Lomami). Since then skins, specimens and photos have been recorded by the Kyoto Dai research projects, the TL2 exploration/conservation and Kokolopori Bonobo projects. In mature individuals the crown to the root of the tail is dark mahogany agouti, contrasting strongly with white buttocks, brow-patch, chest and chin. Throat and cheeks are orange. Mature male buttocks are swollen and of the same incandescent blue as the testicles. Dorsally the tail varies from very dark to pale grey, ending in a prominent black tufted tip. For much of its length the underside of the tail is white but a tapered black strip extends 50mm from the anus.

DISTRIBUTION A scatter of records from NE Congo basin, S of Congo R.

HABITAT Thickets within secondary forest and swamp forest along small rivers. Lower levels are preferred and reportedly never seen in the canopy or subcanopy. Fragmented ranges.

FOOD Fruits, young leaves and shoots of monocot gingers and arrowroots and the fruits of low-level trees, shrubs and vines (detailed studies initiated by A. Lokasola, Kokolopori scientist).

BEHAVIOUR Local hunters have described groups of up to 30 animals. Other observers have noted single-male groups numbering 2–15. Association with *C. (cephus) ascanius* reported.

ADAPTATIONS Molars display heavy wear at the back at an early age while upper incisors are unusual in being weak and splayed. This unique combination suggests separation of the jaw's functions. The Dryad Monkey shares some dental resemblances, a

preference for low levels and a sit-tight hiding strategy with De Brazza's Monkey. Most likely derives from the very earliest stock of *Cercopithecus* monkeys, perhaps more distantly to *Chlorocebus*.
STATUS An accomplished 'hider', Dryad Monkeys may be more widespread than is currently known. However, observers have noted that the voracious and uncontrolled bushmeat trade is rapidly depleting all species near roads and rivers. The Dryad Monkey seems to be a rare relict species group with a poor capacity to disperse or colonise/recolonise. All populations are of the greatest scientific interest and their effective conservation is of the highest priority. Currently rated as critically endangered by IUCN.

SALONGO MONKEY *Cercopithecus (dryas) salongo*

MEASUREMENTS See *C. (d.) dryas*.
RECOGNITION In 1977 *C. salongo* was named from the incomplete skin of a monkey reportedly taken from south and west of known Dryad Monkey localities. This taxon has been described as having a white brow band with elongated tufts above the temples separated from white or cream cheeks by a tapered black line. The crown, back, sides and upper limbs are speckled yellowish olive-grey. White underside, black lower limbs and black-tipped tail as in Dryad Monkeys but with a black spot on the white underside of the tail, well separated from the anus.
DISTRIBUTION Animals that appear to match this supposed taxon have been reported from more westerly localities (all south of the Congo R.), but observations and distribution records for all *C. (dryas)* forms needs disciplined documentation overall.
For Habitat, Food, Behaviour, Adaptations and Status see Dryad Monkey profile above.

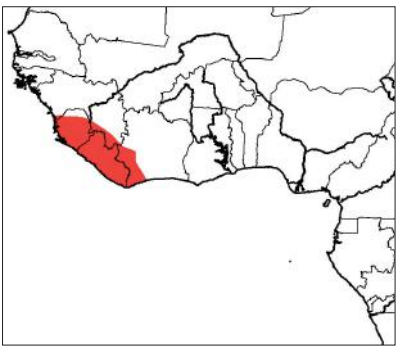
DIANA MONKEYS *Cercopithecus (diana)* group

Formerly treated as two subspecies of *C. diana*, further study has suggested each form is sufficiently distinct to be treated as a full species.The name derives from Linnaeus fancying he saw a crescent moon outline in the brow hairs of a preserved skin! (Diana was a classical moon goddess.)

DIANA MONKEY

Cercopithecus (diana) diana

OTHER NAMES Fr. *Cercopithèque diane*.
Ger. *Dianameerkatze*.
MEASUREMENTS HB 440–450mm (♀), 520–610mm (♂). T 700–900mm. W 2.9–4.9kg (♀), 4.0–6.3kg (♂).
RECOGNITION An agile, long-limbed monkey with strongly contrasting colours and pattern. The dark grey of the body graduates to black down the outer legs and arms. Chest, chin and outer cheeks are white and a white thigh-stripe. The lower back is deep mahogany brown. The back of the thighs and inner legs are deep russet, concealing a blue scrotum in males. The brow-band varies in conspicuousness. The face is black. Loud calls of male Diana Monkeys are very distinctive volleys of reverberating hacks ending in an explosive 'pyow'.



Diana Monkey

These are uttered while stationary or while running a fast arboreal circuit, punctuated by leaps against branches and shaking of foliage.

DISTRIBUTION From Sierra Leone and SW Guinea (Seredou) to W Côte d'Ivoire. From sea level up to 1,400m (on north side of Mt Nimba). Now in small patches.

HABITAT An almost entirely arboreal species dependent on continuous canopy and with a strong preference for high-canopy primary rainforest. Also found in mature secondary, riverine and semi-deciduous forests and galleries. Densities vary greatly, but when the river island of Tiwai (12km^2) received protection, between 30 and 50 Diana Monkeys were recorded per km^2.

Diana Monkey

FOOD Primarily fruits and seeds. Leaves and, incidentally, invertebrates and small vertebrates are also taken.

BEHAVIOUR Groups of approximately 6–8 females and their young are accompanied by one adult territorial male, total 14 (10–50). Diana Monkeys feed and rest in a very dispersed pattern, reinforced by female hierarchies. Groups rally to male loud calls, typically uttered in the morning, after resting and at any disturbance. Females make distinctive trilling contact calls, single chirps and appeasement barks. Territories of 100–200ha are travelled over daily. Alert monkeys, quick to flee from danger. No pronounced breeding season. Young, born a light, brownish grey, acquire black-and-white contrasts over 6 months or so. Mature at 5.5 years of age.

ADAPTATIONS Bright colours and linear contrasts at the rear end of this monkey give visual emphasis to small changes in posture by creating contrasting, angular, geometric configurations. This 'whole-body' patterning is specifically adapted to long-range signalling in dispersed social units. Dominant animals generally stand with stiff legs and prefer to posture facing down a sloping branch.

STATUS Diana Monkey groups make daily traverses over their relatively large territories in a characteristically noisy and conspicuous manner that renders them particularly vulnerable to hunters with shotguns. In the centre of the Diana Monkeys' range in Liberia there are virtually no constraints on large-scale bushmeat hunting, using modern firearms, lights, vehicles, fridges and processing techniques. Diana Monkeys are a popular prey because they are easy to find and both their meat and skins fetch high prices. In common with all other Upper Guinea biota, the greatest threats to survival come from logging of the trees that make up their high-canopy habitat and from hunting. Rare in 1960, all populations continue to decline. Diana Monkeys are protected in several reserves and National Parks but are extensively poached. Without specific programmes devoted to their survival and the preservation of their habitat they face extinction. Listed as Class B (African Convention), Appendix I (CITES), vulnerable to extinction (IUCN).

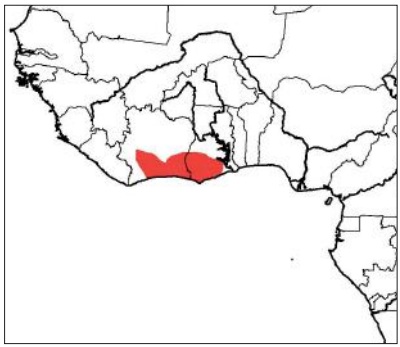
ROLOWAY MONKEY

Cercopithecus (diana) roloway

OTHER NAMES Fr. *Diane roloway*.
Ger. *Rolowaymeerkatze*.

MEASUREMENTS HB 420mm (♀), 510–630m (♂). T 510–830m. W (est.) 3–5kg.

RECOGNITION Differs from *C. (d.) diana* in being altogether lighter in colouring and in lacking a black goatee. Face and lower lip black. Crown, anterior back, sides, shoulders and upper thighs freckled grey graduating to black down the outer legs and arms. Inner forearms, chest, beard and outer cheeks and thigh-stripe are white. Lower back is russet to ochre. The back of the thighs and inner



Roloway Monkey

legs vary from yellowish cream to bright russet. Wide, white brow-band. Roloway Monkeys have been recorded associating closely with Geoffroy's Colobus, catching insects dislodged by their passage. Territorial calls of male Roloway Monkeys are very loud and carry far. Like Diana Monkeys, males also advertise their presence by noisily bouncing against and shaking foliage.

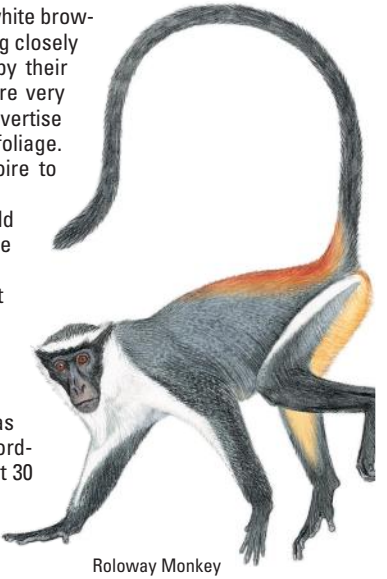
DISTRIBUTION From Sassandra R. in central Côte d'Ivoire to Kakum NP in Ghana.

HABITAT An arboreal species limited to primary and old secondary high-canopy rainforest, an increasingly rare habitat.

FOOD Ripe fruits, seeds, buds and fresh leaves, but invertebrates make up as much as a quarter of their diet.

BEHAVIOUR Territorial, one-male groups of 15–20 individuals forage in a very dispersed pattern and in one well-studied group of 15 animals the total range was 189ha. No obvious breeding season but copulations recorded peaking in July. In captivity known to live for at least 30 years.

ADAPTATIONS As in Diana Monkeys, bright colours and distinctly linear markings are associated with emphatic postures and displays. These assist long-range visual signalling in a canopy-dwelling species.



Roloway Monkey

STATUS Roloway Monkey groups are particularly easy to hunt and poach because the males are noisy and easily located. Once common and widespread within its range, most populations have been exterminated in relatively recent times. Arguably one of the most beautiful of African mammals and certainly one of Ghana's crown jewels, Roloway Monkey will assuredly become extinct if the national governments' apathy about conserving natural assets continues. The species survives under nominal protection in the Krokusa hills, in Ankasa Reserve and Nini-Suhien and Kakum National Parks in Ghana and in Tanoe Forest in Côte d'Ivoire. Listed in Appendix I (CITES) and by IUCN as endangered.

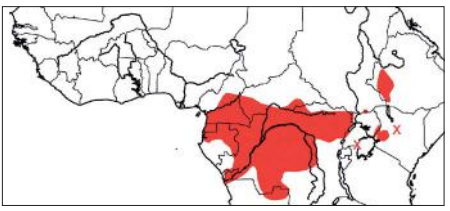
DE BRAZZA'S MONKEY

Cercopithecus neglectus

OTHER NAMES Fr. *Cercopithèque de Brazza*. Ger. *Brazzameerkatze*. Swah. *Kalasinga*.

MEASUREMENTS HB 450mm (390–543mm) (♀), 560mm (484–600mm) (♂). T 470–784mm. W 2.5–5.0kg (♀), 4.8–8.0kg (♂).

RECOGNITION A long-tailed and grey-backed guenon with orange brow and white beard. Forearms, hands, feet, belly and tail are black. The inner surfaces of the thighs and buttocks are white. There is a white stripe down the thigh. females are smaller than adult males. The young change colour from infant brown to grey with rich russet suffusions to the head and rump. De Brazza's Monkey habitually retreats at the least disturbance, slipping behind a branch or crouching in the foliage. When a group is disturbed the male may threaten or give a chattering croak followed by single croaking barks. Undisturbed, it is a quiet, exceptionally slow, deliberate and intensely observant monkey.



De Brazza's Monkey

DISTRIBUTION From S Cameroon and equatorial Guinea through most of the Congo basin to Rwenzori Mts, except for Virunga Mts zone. It also occurs in the vicinity of the Elgon and Debasien Mountains and in S Ethiopia (R. Omo).

HABITAT A river-oriented monkey moving away from the river only to visit a major food source (such as fruiting fig trees). The riverine habitat spans all forest types, from lowland and swamp forests to semi-deciduous, *Acacia*-dominated and lower montane galleries. In this zone the ground is

De Brazza's Monkey

frequently flooded for long periods, which renders it an exceptionally safe refuge from terrestrial predators (thorny undergrowth also deters eagles). De Brazza's Monkey sleeps, hides and travels at low levels (below 5m) but juveniles generally avoid descending to the ground. Home-ranges frequently follow only one bank of a river, they are therefore linear and can total over 1km in length and cover up to 10ha, although in rich habitats they cover no more than 5–6ha. While the central zone of a group's range is exclusive there may be minor overlaps with the ranges of neighbouring groups.

FOOD Half to three-quarters of the diet comprises fruits and seeds. However, shortfalls in fruits and seeds can be offset by taking leaves. This ability to take a significant proportion of leaves permits the monkey to remain within a small but secure home-range throughout the year. It will feed on fruits in the early morning, and, as temperatures rise, it descends to lower levels where it feeds mainly on leaves, herbs and invertebrates. The latter are mainly insect larvae and pupae uncovered by meticulous gleaning of the forest floor and overgrown tree trunks. Groups of de Brazza's Monkeys travel between 300 and 500m in a day but they may remain so close to a tree throughout its fruiting season that they are effectively sedentary.

BEHAVIOUR One or more females are accompanied by an adult male. Where selective predation on males is high and the habitat disturbed (as in parts of its range in E Africa) the total numbers in an aggregation can rise up to 35. More normal averages range between two and six individuals. The male utters a deep, humming boom most frequently in the early morning, after any disturbance and whenever there is any change in the direction of travel. Its effect is to draw the group together. Group members are observed to remain 2–100m apart and they utter a quiet croaking grunt to keep in touch. De Brazza's Monkeys scent-mark and males are particularly active in this respect. Although temporary encounters and mixing with neighbouring groups may evoke little more than much excited grunting or croaking, adult males are generally intolerant of other adult males (and other guenon species) at their food trees and will force them to retreat.

ADAPTATIONS De Brazza's Monkeys can remain immobile for up to 8 hours. However, regrouping depends on visual signals as well as the male's hums and loud calls. The male acts as both defender and beacon for his group and must switch from 'hider' to 'advertiser' as soon as danger has passed. Both the back and front ends of de Brazza's Monkey reveal matching colours and pattern, effectively transmitting a double signal, as during rallying behaviour when, between violent shakings of vegetation, he will reverse his position (showing either his white beard or his white buttocks, see colour illustration on p.140).

STATUS De Brazza's Monkey is rare or endangered in Kenya, Ethiopia and Uganda because its habitats are being eroded by cultivation or clearance of trees. In some other parts of its very extensive range it is still common.

MONA MONKEYS *Cercopithecus (mona)* group

OTHER NAMES Fr. *Mone*. Ger. *Meerkatze*.

RECOGNITION Medium-sized to small, arboreal monkeys with a grizzled back and small dark hands and feet. The face is enlarged by pale cheek ruffs and the ears are tufted. The skin surrounding the eyes is dark grey or blue while that around the mouth is depigmented. The underside is generally light-coloured with sharp contrasts running down the forearms. The tail is long, with a dark tip and lighter midsection. Genitals are inconspicuous.

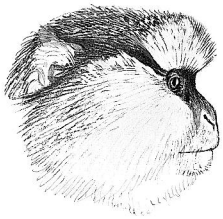
GEOGRAPHIC VARIATION Mona Monkey, *C. (m.) mona;* Campbell's Monkey, *C. (m.) campbelli*; Lowe's Monkey, *C. (m.) lowei*; Dent's Monkey, *C. (m.) denti*; Wolf's Monkey, *C. (m.) wolfi*; Crowned Monkey, *C. (m.) pogonias*. In spite of close family resemblance, recent genetic studies have shown that chromosome numbers differ from species to species (66 in *C. (m.) campbelli*, 68 in *C. (m.) mona*, 72 in *C. (m.) wolfi* and *C. (m.) pogonias*). These differences suggest that the group has evolved over a protracted period and that *C. (m.) pogonias* and *C. (m.) wolfi* are more recently evolved than *C. (m.) campbelli* and *C. (m.) lowei*.

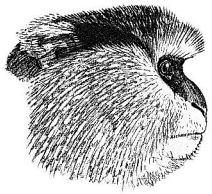
DISTRIBUTION Strictly limited to the main lowland rainforest blocks (although they may survive in patches that have become detached as a result of recent forest clearance). The main constraint limiting their distribution is seasonality of the climate. They are absent from forests subjected to strong seasonal fluctuations in rainfall or temperature. Similar constraints have inhibited their colonisation of forests at higher altitudes and latitudes. The more recently evolved species, *C. (m.) pogonias* and *C. (m.) wolfi*, occupy the centre of the group's range. The easternmost race of *C. (m.) wolfi* has some resemblances to its neighbour, *C. (m.) denti*. While *C. (m.) denti* undoubtedly bears some relationship to this advanced species, it has a much older link with *C. (m.) campbelli* in the far west. This complex 'ring' of populations, in which conservative species occupy the margins, implies that monas may be actively undergoing a group radiation.

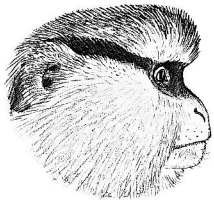
HABITAT Almost wholly arboreal, most mona monkeys rely on dense, relatively unbroken canopy in primary, secondary or well-developed gallery forests.

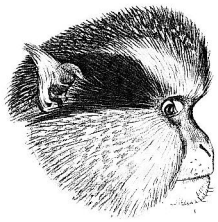
FOOD Fruits and up to 20% invertebrates. Foliage and other plant parts are less significant. Feeding routines begin with bulk fruit intake in the morning followed by insect-hunting in the shade during the heat of the day and a return to fruits in the afternoon.

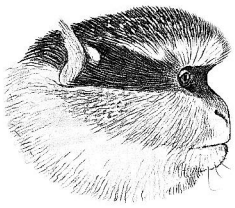
BEHAVIOUR Groups of 5–20 animals are accompanied (often at some distance) by a single territorial male who serves as a lookout rather than a 'protector' for the rest of the group. All monas are very fast, agile monkeys that never stray far from dense vegetation in which they can hide (eagles were the main danger before humans became the principal predator of both monkeys and eagles). Monas enact highly ritualised sequences of movement and posture while vocalising. Body postures

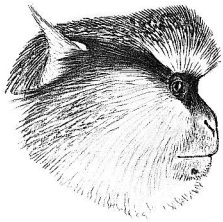

Campbell's Monkey


Lowe's Monkey


Mona Monkey


Crowned Monkey


Wolf's Monkey


Dent's Monkey

alternately expose and conceal the bright face and chest patterns. Exceptionally active, curious monkeys, monas frequently interact with, and respond to, fellow group members, other primates and even squirrels, birds and insects.

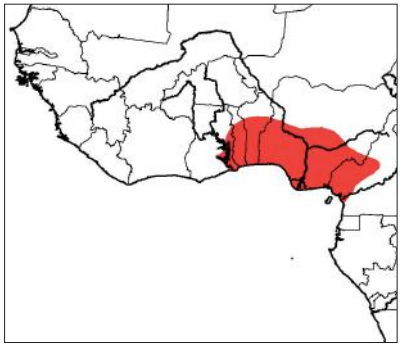
Female monas mature and begin breeding at 2.5–4 years of age. Gestation lasts 6 months and young become independent relatively early.

ADAPTATIONS Mona monkeys have small hands and feet with exceptionally flexible ankles and wrists, well suited to their fast arboreal gymnastics. Their broad hands, with well-developed thumbs, allow them to readily catch and dismember active insects, such as grasshoppers, flies and cicadas.

STATUS Fecundity, agility and an unparalleled ability to conceal themselves are among the characteristics that have enabled monas to offset depredation from a wide range of predators, including humans. Their small size used to make them less attractive to hunters but with cheap guns and ammunition now available they are heavily hunted throughout their range. Widespread forest clearance has greatly reduced numbers in some areas.

MONA MONKEY

Cercopithecus (mona) mona

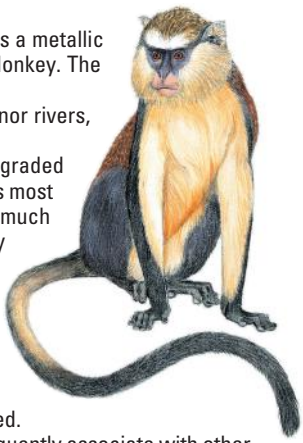


Mona Monkey

OTHER NAMES Fr. *Mone*. Ger. *Mona-Meerkatze*.

MEASUREMENTS HB 340–457mm (♀), 410–630mm (♂). T 520–730mm. W (2.1–4.3kg) (♀), (3.2–5.7kg) (♂).

RECOGNITION A long-tailed monkey with a mahogany-brown back, cream-coloured underparts, chest and inner surfaces of the limbs. The rounded, furry head has an off-white brow-band and pale cheek-fur that contrast strongly with the blue-grey mask of bare skin surrounding the eyes. The lower limbs are black on the outer side. Two oval patches of white fur flank the tail on the hips and would appear to resemble upwardly displaced, exaggerated ischial callosities. They are unique to this species and noticeable even from a distance. The Mona Monkey is very vocal and utters a want call which has a metallic grating quality, harsher than equivalent calls made by Lowe's Monkey. The male alarm call is a two-phase 'ooé'.



DISTRIBUTION Focused on the R. Niger delta and surrounding minor rivers, from the R. Volta to the R. Sanaga.

HABITAT A lowland-forest species that inhabits all but the most degraded and upland forests within its regional range. The Mona Monkey is most abundant close to riversides and follows forest galleries out into much drier country in central Nigeria. It is the commonest monkey throughout the vast mangrove forests of the R. Niger delta.

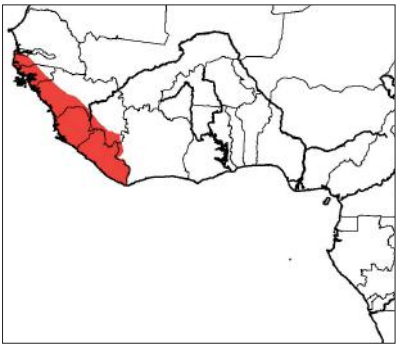
FOOD A true frugivore that also takes invertebrates. Invertebrates are likely to be particularly important in the diets of mangrove-dwelling populations. One study in Benin recorded 76% fruit, flowers and seeds and about 10% insects.

BEHAVIOUR Groups averaging 12 animals are accompanied by a single adult male but larger aggregations have also been recorded. They can live at high densities when not heavily hunted. They frequently associate with other monkey species. Between the Cross R. and R. Sanaga such mixed parties include the closely related *C. (m.) pogonias*, while in the R. Volta valley they include *C. (m.) lowei*. The greater numbers of *C. (m.) pogonias* and occasional hybrids suggest that *C. (m.) pogonias* might be forcing *C. (m.) mona* into a gradual retreat in Cameroon.

ADAPTATIONS Lowe's Monkey and the Mona Monkey might have first diverged because they were separated by much drier climatic phases. At such times true forest conditions would have contracted to delta mangrove swamps and narrow riverine strips, the habitat most favoured by the Nigerian mona. It would appear that the Mona Monkey's intrusion into the R. Volta valley system is the product of a westward expansion assisted by this species' relative tolerance of drier conditions.

If the white hip discs (that are exclusive to this species) mimic ischial callosities then they might be interpreted as signals promoting social cohesion because ischial callosities are associated with the gesture of 'presenting', which helps to appease aggressive behavior. It would be interesting to learn of any behaviour that might display these species-specific hip discs in a social context.

STATUS In spite of massive destruction of its habitat and relentless hunting pressure, the Mona Monkey remains a fairly common and widespread species.



Campbell's Monkey

CAMPBELL'S MONKEY

Cercopithecus (mona) campbelli

OTHER NAMES Fr. *Mone de Campbell*.
Ger. *Campbell-Meerkatze*.

MEASUREMENTS HB 360–430mm (♀) 420–550m (♂). T 490–850mm. W 2.0–4.5kg (♀), 3.2–5.5kg (♂).

RECOGNITION A long-tailed, arboreal monkey with dark-grey hindquarters, belly and lower forearms, graduating into a tawny-brownish grizzle on the shoulders and crown. The pale cheek-ruffs are broad and circular, with scarcely a trace of annulation or grizzling, and are separated from the broad white brow-diadem by the narrowest of temporal streaks. The ear-tufts are also plain white or cream. The facial pattern closely resembles that of Dent's Monkey.

DISTRIBUTION From the R. Sassandra valley west to Gambia.

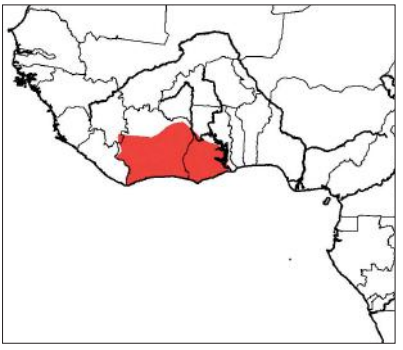
HABITAT A wide range of forests, including mangroves and narrow galleries. Campbell's Monkey has readily taken to secondary growth fringing gardens and fields.

FOOD Mainly fruits with flowers and insects.

BEHAVIOUR Resembles other mona species in having small, single-male groups and small ranges in relatively rich habitats.

ADAPTATIONS The dull colouring of this species is probably cryptic and may reflect the more exposed and dangerous conditions under which it lives relative to other monas.

STATUS Although range and numbers are greatly depleted, Campbell's Monkey is still widespread.



Lowe's Monkey

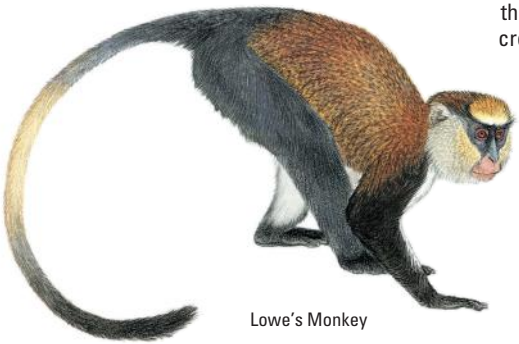
LOWE'S MONKEY

Cercopithecus (mona) lowei

OTHER NAMES Fr. *Mone de Lowe*.
Ger. *Lowe-Meerkatze*.

MEASUREMENTS HB 360–430mm (♀), 420–550mm (♂). T 540–850mm. W 1.8–5.0kg (♀), 3.2–5.8kg (♂).

RECOGNITION A long-tailed, arboreal monkey with grizzled brown back, dark grey hindlegs and rump, black outer arms, tail tip, hands and feet. Underparts are white. The finely grizzled cheek-fur pales to form a sharp contrast with the blue-grey eye-mask that typifies all monas. A similar narrow margin edges the oval orange-yellow brow-band. Ear-tufts are grizzled and often yellowish. The temples are marked by a broad black band that separates



Lowe's Monkey

the light cheeks and ears from the dark crown and orange brow. This very vocal monkey often betrays its presence with an explosive sneeze of alarm or a nasal 'ooeeoo' contact call. Males utter a three-phase 'ooahoo'.

DISTRIBUTION The rainforest zone between the R. Sassandra and R. Volta.

HABITAT Most forest types; primary, secondary and galleries, but not common in marshy areas or mangroves. Lowe's Monkey is less exclusively arboreal than most monas and has no close association with riverbanks or water. It stays close to cover and generally avoids exposure.

FOOD Mainly fruit; pulp of oil-palm seeds, figs, *Cola*, *Baphia* and garden fruits have been recorded, and flowers. Insects are frequently hunted but little interest is taken in vertebrates or leaves.

BEHAVIOUR Groups average 10 animals and comprise a single adult male with about four adult females and their young. Home ranges extend from about 1.5 to 3ha. But a group of 5–6 individuals in degraded, lagoon-side forest and gardens ranged over 14ha. Gestation lasts about 6 months and the species shows a distinct birth-peak in December–January.

ADAPTATIONS The genetic distinctness of this species from *C. (m.) mona* is evident from its coexistence in the R. Volta valley with no sign of hybridisation. However, where Lowe's Monkey and Campbell's Monkey overlap, between the R. Sassandra and R. Nzo, the former is dominant in the moister south while the latter is commoner in the marginally drier north. Hybrids do occur but a high degree of separation in the absence of any obvious barrier suggests a relatively ancient genetic divergence. It has been suggested that monas originated as a distinct group in West Africa. As the most 'generalised' of the monas, with the least well-defined coat pattern and a low chromosome count, Lowe's Monkey would appear to be the most conservative of all living mona monkeys. Its survival and study is important for understanding the mona radiation in particular and the adaptive trends of forest primates in general.

STATUS Although habitats and numbers have been greatly reduced this species remains common and widespread.

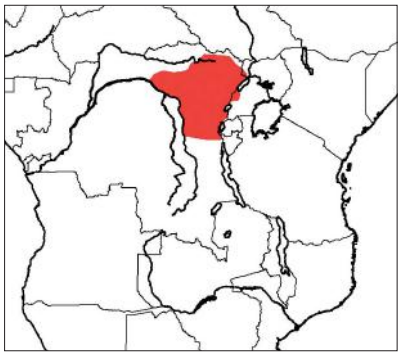
DENT'S MONKEY

Cercopithecus (mona) denti

OTHER NAMES Fr. *Mone de Dent*.
Ger. *Dent-Meerkatze*.

MEASUREMENTS HB 400–700mm. T 700–900mm. W 2–3.7kg (♀), 3.6–5kg (♂).

RECOGNITION A long-tailed, arboreal monkey with a brilliant contrast between the white belly and dark back. The white inner limbs also contrast strongly with the black arms and grizzled brown legs. The back is a rich, grizzled mahogany brown; the feet are black and the tail is grey with a black tip. The face mask is blue-grey with a depigmented muzzle. The circular cheek-ruffs are yellowish off-white and the brow a dirty white.



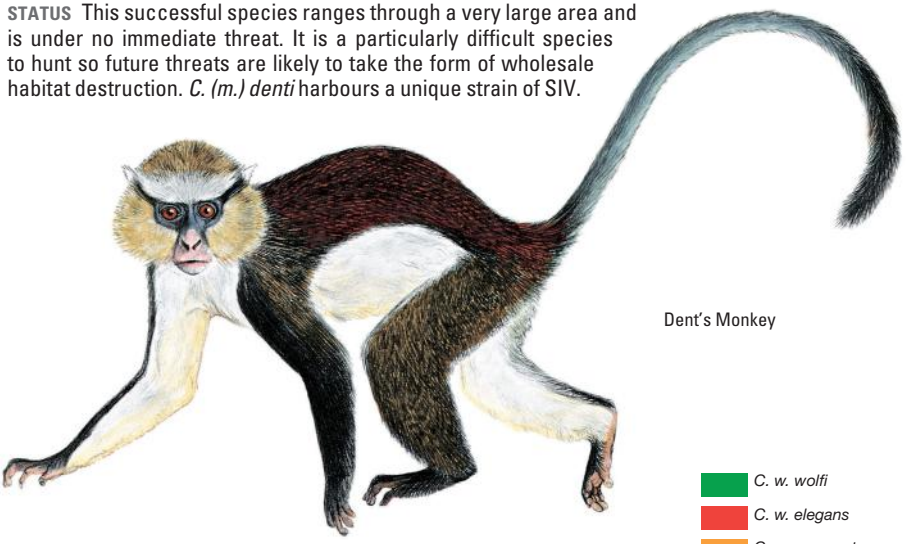
Dent's Monkey

DISTRIBUTION Between the R. Lualaba, Congo R. and R. Itimbiri and the Rwenzori foothills.

HABITAT Lowland forests with a preference for high-canopy mixed forest. Tends to avoid swamp forest and large river margins.

FOOD Fruits, flowers and invertebrates (especially caterpillars). Shoots and leaves are more marginal foods.

BEHAVIOUR Dent's Monkey lives in groups of up to 12 animals with a single adult male. They frequently associate with much larger groups of Red-tailed Monkeys. When alarmed, the group readily disperses in twos and threes in different directions and will freeze in knots of vegetation for long periods. The male's booming loud call brings the group members together again. Dent's Monkey has been implicated in the epidemiology of Yellow Fever and other viral diseases.
ADAPTATIONS Resemblances between Dent's Monkey and Campbell's Monkey suggest that a much more homogenous mona population was once dispersed right across the rainforest zone. There are also resemblances with Wolf's Monkey *C. (m.) wolfi* (some taxonomists treat Dent's Monkey as a race of *wolfi*).
STATUS This successful species ranges through a very large area and is under no immediate threat. It is a particularly difficult species to hunt so future threats are likely to take the form of wholesale habitat destruction. *C. (m.) denti* harbours a unique strain of SIV.

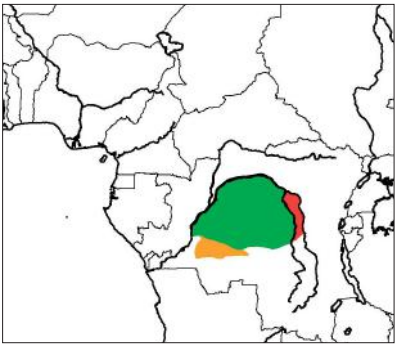


Dent's Monkey

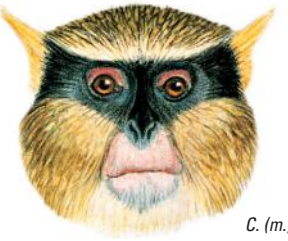
WOLF'S MONKEY

Cercopithecus (mona) wolfi

OTHER NAMES Fr. *Mone de Meyer*.
Ger. *Wolf-Meerkatze*.
MEASUREMENTS HB 450–510mm. T 600–820mm. W 1.8–3.7kg (♀), 2.6–5.1kg (♂).
RECOGNITION A long-tailed, arboreal monkey with a lighter dorsal stripe down the dark, grizzled back. Hindquarters are sharply differentiated in colour (reddish or orange) while the outer forearms are black. On each side of the eye-mask, dark skin and



Wolf's Monkey



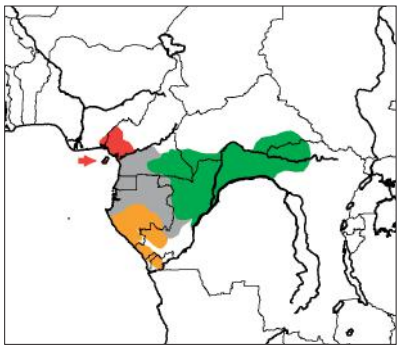
C. (m.) wolfi wolfi

shorter fur extend back across the upper cheeks and temples to the ears, which have brightly coloured tufts. The fur on the lower cheeks is longer and lighter. A relatively narrow and light-coloured brow-diadem extends back to the ears.
GEOGRAPHIC VARIATION *C. (m.) w. wolfi* (S Congo basin between Congo R. and R. Kasai): slate-grey back, white underside, orange ears, orange or reddish hindlegs and lateral stripe. *C. (m.) w. elegans* (short stretch between upper reaches of R. Lomami and R. Lualaba): dark back, white underside, grey hindlegs, white ear-tufts, very narrow brow stripe. *C. (m.) w. pyrogaster* (forests south of R. Kasai): dark back, dark red hindlegs, red ear-tufts and underside.
HABITAT Lowland rainforests of the S Congo basin, with a preference for high-canopy primary and secondary forests.
FOOD Fruits, flowers and invertebrates.
BEHAVIOUR Closely resembles that of Crowned Monkeys *C. (m.) pogonias*. The typical display is a stiff-legged, raised-rump posture in which the distinctively coloured hindlegs form an eye-catching angle with the tail and lowered torso. Whereas most guenons have broad ruffs of cheek-fur that make their heads look larger, this species has flattened fur in front of the ears. As the ears are elaborated with a bright flash of colour it would appear that the ears and ear movements are important in communication. This peculiar flattening correlates with a ritualised 'head-flagging' behaviour which is typical of several guenon species and would appear to originate in avoidance of eye-contact gestures (the commonest form of mammal appeasement behaviour). In Wolf's Monkey eye-contact avoidance is made more emphatic by turning the head aside to give more of a profile view than in most other species (a gesture that is taken a step further in the Crowned Monkey).
STATUS A widespread and common species that has nonetheless suffered considerable reduction in numbers due to commercialisation of the bushmeat trade and increasingly dense settlement in parts of its range.

CROWNED MONKEY

Cercopithecus (mona) pogonias

OTHER NAMES Fr. *Cercopithèque pogonias*.
Ger. *Kronenmeerkatze*.
MEASUREMENTS HB 340–480mm (♀), 370–550mm (♂). T 480–870mm. W 2.2–3.8kg (♀), 3–5.1kg (♂).
RECOGNITION Relatively small, long-tailed, arboreal monkey with grizzled sides and hindlegs and black outer arms and feet. A striped crest runs along the centre of the crown and the ear-tufts are very



Crowned Monkey

prominent and usually pointed. The underside is orange, yellow or white. The Crowned Monkey is exceptionally agile and vocal.

GEOGRAPHIC VARIATION *C. p. pogonias* (R. Cross to R. Sanaga and Bioko I.): grizzled khaki sides and thighs, black dorsal stripe, short, yellow-grizzled crown stripe, yellow undersides and ear-tufts, yellow-flecked black feet. *C. p. grayi* (S Cameroon to central Africa north of Congo R.): grizzled chestnut back and thighs, medium yellow crown stripe, orange to yellow underside and ear-tufts, yellow-flecked black feet. *C. p. nigripes* (R. Ogooué basin south to Congo R.): grizzled grey-olive sides and thighs, grey dorsal stripe, broad, creamy-white crown stripe, variable deep orange to white underside and ear-tufts, jet-black feet.

DISTRIBUTION Central African forest zone from Cross R. to Congo R. and R. Itimbiri.

HABITAT Commonest in mature forests and in upper strata but also in secondary forest and gallery forests extending well into savanna regions.

FOOD Fruits (80%) and invertebrates. Crowned Monkeys very rarely take leaves or buds, preferring soft, pulpy, red or yellow fruits. Bulk fruits are taken in the morning and late afternoon while insects, especially beetles and caterpillars, are hunted in the middle of the day.

BEHAVIOUR Groups of 8–20 (mean 10) animals with a single dominant male occupy home-ranges of 0.5–1km^2. Crowned Monkeys are very vocal. The dominant male's booming call serves to rally group members after dispersal or a disturbance and more than one male may utter the territorial loud call, or hack. Both sexes make the strange miaow that is the typical cohesion call. This, and other shorter, whining calls are intragroup calls and capable of much modulation. They have a versatility of expression that would appear to range from 'inviting' and 'inquisitive' to repelling and aggressive. Group members readily disperse and reaggregate, and usually sleep huddled together in family groups.

ADAPTATIONS The striking Mohican crest that earns this species its name is marked by strong contrasts of black and white or black and yellow that form a pattern that is most striking when viewed from the side. Like their close relative Wolf's Monkey, Crowned Monkeys perform a ritualised head display involving frequent jerking turns to left and right.

STATUS It would seem that the *pogonias* lineage would have had to cross the Congo R. along its lower, very swift-flowing reaches. Such an origin could have resulted in a narrow genetic bottleneck but one that has clearly been followed by outstanding success. Indeed *C. (m.) pogonias* may yet be actively expanding and displacing *C. (m.) mona* in SW Cameroon.

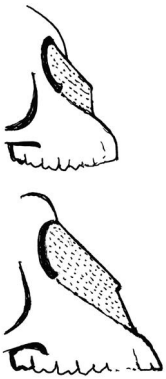
LONG-FACED MONKEYS *Cercopithecus (hamlyni)* group

Molecular genetics suggest that these largely terrestrial forest monkeys represent an ancient phylogenetic link between de Brazza's Monkey, gentle monkeys *(nictitans*) and mona monkeys (*mona*), even while sharing only a few characteristics with each of the three lineages. Other, mostly non-molecular, resemblances have suggested behavioural and anatomical links with *Allochrocebus* (blood proteins, cranial proportions, molars and blue balls). The *Cercopithecus* allocation in terms of genes seems robust, yet the numerous *Allochrocebus* similarities present two possibilities. One is quite remarkable levels of convergence, which alone deserve study; the other is that the long-faced monkeys (*hamlyni*) represent some stabilised inter-generic hybrid event that preceded emergence of the two extant species.

Examining how niches might open up for forest monkeys, ecologist Steve Gartlan showed that sensory channels are integral to the elaboration of niches. For long-faced monkeys, living in dense vegetation at ground level, visual range contracts and sound attenuates fast. Ever-present terrestrial predators make both bold visual and loud vocal signals even more dangerous. In compensation, long-faced monkeys, besides being very quiet, have retrieved or retained a channel that has been broadly suppressed in arboreal monkeys – scent-marking. Both species have elaborated tracts of apocrine glands on their chests, which both sexes, of all ages, wipe very frequently on their surroundings. Under a rainfall of over 1,250mm, continuous herbaceous growth changes physical surroundings while the rain washes away previous markings. In such circumstances a group of monkeys must 'map' out their small, densely obstructed home-range by very frequent scent-marking. Long-faced monkeys are therefore demonstrable scent broadcasters. That they are also receptors can be appreciated by comparing the nasal area of a non-olfactory arboreal species with that of a long-faced monkey, where the most prominent species-specific

cranial feature is a greatly elevated, elongated and compressed bony nasal ridge. Furthermore, this ridge is given extraordinary visual emphasis by being advertised in most individuals and populations with a crisp, straight and narrow stripe of pale skin under white fur. In all other respects these are quiet, largely terrestrial monkeys with dull grey, black and brown colours.

Whatever the conditions in which these monkeys survived or evolved in the past, their present declining existence in isolated patches of suitable habitat begs for much more intensive research. Understanding their niche (and their genetic relationships) within the larger context of other primates and other mammals, large and small, could be a significant step forward in knowledge of evolution and ecological dynamics in African rainforests.



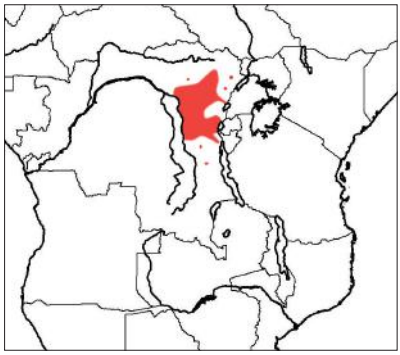
Nasal area (stippled) in skulls of (*top*) arboreal guenon *C. (mona)* and (*above*) long-faced guenon *C. (hamlyni)*.

OWL-FACED MONKEY *Cercopithecus (hamlyni) hamlyni*

OTHER NAMES Hamlyn's Monkey. Fr. *Cercopithèque de Hamlyn, Cercopithèque à tête de hibou*. Ger. *Eulenkopfmeerkatze*. Lega dialect *Mutuba*. Kahuzi dialect *Fuya*.

MEASUREMENTS HB. 430–480mm (♀), 500–630mm (♂). T 490–630mm. W 2.6–4.5kg (♀), 4.4–7.3kg (♂).

RECOGNITION A thickset, monochrome, grizzled grey monkey with black arms, feet, underside and tail tip. In most individuals and populations the long nose is marked with a vertical white stripe and pale cream horizontal brow-ridge. The fur is exceptionally fine, dense and long. There is bare blue skin on the buttocks and, in the male, the blue skin extends onto the genital area covering both scrotum and penis. Males have very elongated muzzles and are substantially larger than females. The male loud call is a deep boom, otherwise this species is exceptionally quiet and wary.



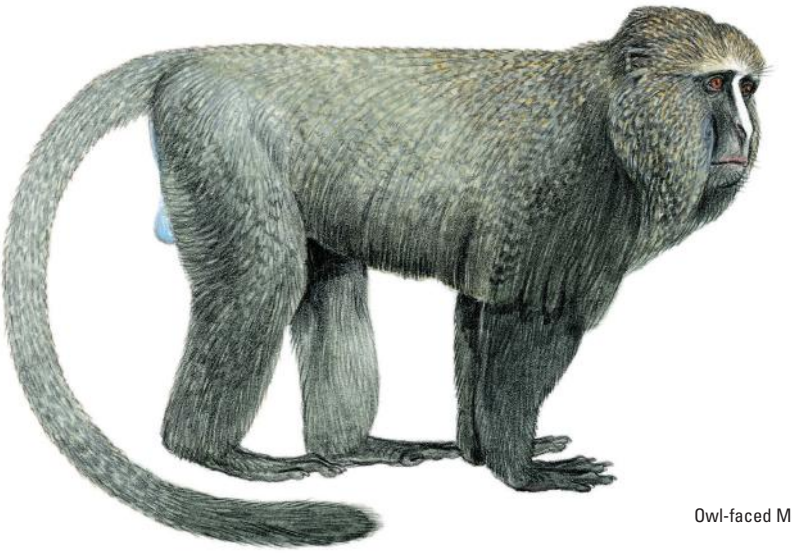
Owl-faced Monkey

GEOGRAPHIC VARIATION On Mt Kahuzi a subspecies, *C. h. kahuziensis*, has been claimed. Supposedly distinguished by the absence of nose-stripe and brow-patch, it is now known that these markings can occur or be suppressed in any part of the Owl-faced Monkey's range. In a volcanic area with local extirpations due to periodic eruptions or gas releases, founder-populations of Owl-faced Monkeys (on Mt Kahuzi or elsewhere) are likely to represent very recent colonists or re-colonists. The most plausible core area for *C. h. hamlyni* is the Itombwe Mts (north-west of L. Tanganyika), where extensive bamboo and montane forests grow on ancient basement rocks. Small numbers of founding colonists might favour *C. hamlyni* in areas like Mt Kahuzi, where as few as six large mammal herbivores occur and Eastern Gorillas and Owl-faced Monkeys are still the only primates.

DISTRIBUTION Wedged between the mountains of the central Western Rift and a stretch of the R. Lualaba, the distribution of this species has long been interpreted as that of a mountain species that spread into lowland forest down the rivers that drain to the west. An opposite argument could be made that a relatively ancient lowland species that tolerated cold, found less competition in wet montane forests. A close correspondence between *hamlyni* distribution and a possible 'Virunga extinction zone' downhill of the volcanoes invites these and other speculations.

FOOD The leaves and shoots of bamboos are known to be eaten. Although new shoots emerge throughout the long wet seasons, these cannot be a year-round staple and numerous other plants are eaten, including roots, leaves, shoots, stems and piths, flowers and lichens, also fungi. Notable foods are the fruits of wild poplar (*Macaranga*), waterberries, *Syzygium*, *Maesa* (*Maesa lanceolata*) and blackberries (*Rubus*).

BEHAVIOUR Known to live in single-male groups numbering less than 10. Intimate knowledge of home-ranges would help explain their legendary ability to evade detection. The impressive-looking



Owl-faced Monkey

males are intensely protective (captive males will come forward at the slightest threat while females and young rush off to hide in a tightly bunched huddle). Communication between these slow, deliberate and monochrome monkeys is primarily vocal and olfactory. The female want call is a whimpering quaver while the male's rallying call is a deep boom. Infants soon suppress the high-pitched chirps typical of other guenon species in favour of quieter calls.

ADAPTATIONS The hands of Owl-faced Monkeys are unique among guenons in the elongation of the phalanges. This is the opposite of a terrestrial trait and, combined with a relatively strong thumb, suggests a powerful grip (as would be needed for climbing among slippery bamboo).

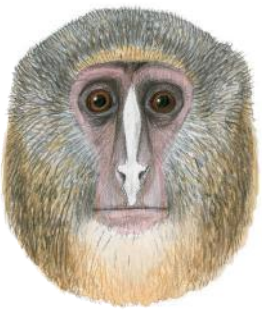
STATUS Extreme crypsis makes this species very difficult to study and census. Although widely distributed, it suffers loss of habitat similar to that suffered by the Eastern Gorilla. There has been no control of hunting in E DR Congo for many years and it is hunters with dogs who pose the main threat. Although distantly related to de Brazza's Monkey, the Owl-faced Monkey belongs to an important, possibly hybrid, guenon lineage and its preservation is of considerable importance. Listed as Class B (African Convention), Appendix II (CITES), vulnerable to extinction (IUCN).

LESULA MONKEY *Cercopithecus (hamlyni) lomamiensis*

OTHER NAMES Fr. *Cercopithèque de Lomami*. Ger. *Lesula meerkatze*.

MEASUREMENTS HB (est.) 400–550mm (♀), 470–650mm (♂). T 400–650mm. W (est.) 4.5–5.5kg (♀), 4.0–7.1kg (♂).

RECOGNITION A newly discovered, grizzled grey and russet monkey with very dark grey arms, feet, underside and near-black tail. The centre line of the nose is white and, like *C. hamlyni*, serves to advertise a structural feature unique to long-faced monkeys. The surrounding face is rather pale, pink, brown or purplish, instead of black, as in *C. hamlyni*. The brow-ridge fur is pale yellowish grizzle and of very variable extent (sometimes vestigial). Like the Owl-faced Monkey, the fur is fine and dense but relatively shorter. There is bare blue skin on the buttocks, scrotum and penis. Males are larger than females and their bright blue genital area covers both the scrotum and penis. An elevated nasal ridge is particularly prominent in males. This, by human perceptions, invests these large-eyed monkeys with a rather wistful appearance. Loud calls, like those of *C. hamlyni*, consist of two or three deep booms of



descending frequency, generated by air released from capacious laryngeal air sacs. These booms are typically uttered at dawn.

DISTRIBUTION Only found between the Lomami and Tshuapa rivers, a low-lying but well-drained tract well to the west of the R. Lualaba (which marks the western boundary of *C. hamlyni*).

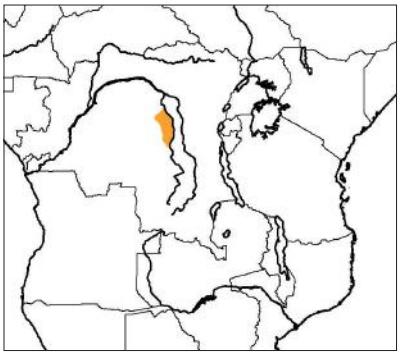
HABITAT Mature, mixed lowland rainforest, including areas where leguminous *Gilbertiodendron* are dominant. Reportedly never found in waterlogged areas.

FOOD Both ripe and unripe fruit, typically foraged on the forest floor. Also terrestrial herbaceous plants, notably seeking out the meristems of Marantaceae.

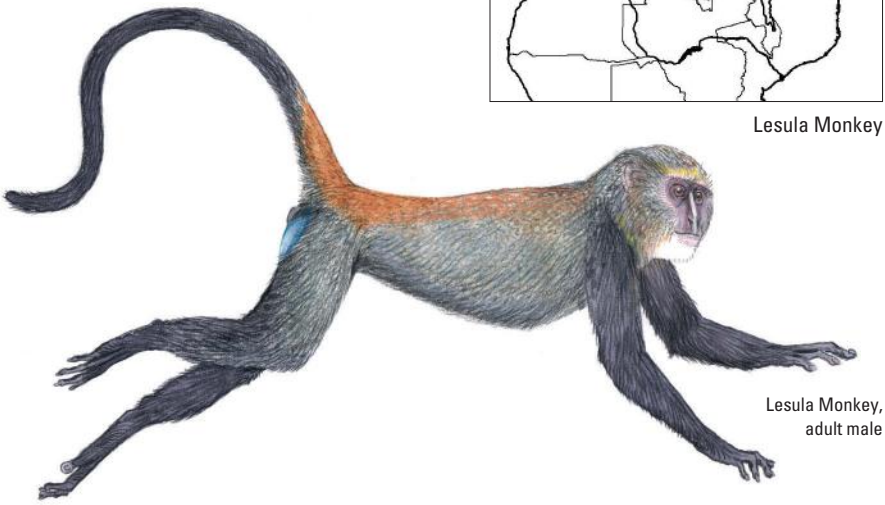
BEHAVIOUR Diurnal monkeys, living in single-male groups of up to five individuals. Females have a variety of discrete calls and their repertoire in general resembles those of *C. hamlyni*.

ADAPTATIONS On superficial examination, the hands of these monkeys resemble those of *C. hamlyni* in having long, curved digits to form a powerful hook, the thumb seems to be well developed but not prominent.

STATUS Hunters catch them with snares, dogs and various weapons. For the time being their range is still outside the normal reach of the piratical Kisangani commercial bushmeat traders but this is rapidly changing and without control of hunting the fortunes of this very localised and scientifically important species could change rapidly. Its best chances lie in adoption of proposals to found a Lomami NP with international funding and support. Not yet listed by IUCN but certainly vulnerable to extinction under present trends.



Lesula Monkey



Lesula Monkey, adult male

GENTLE MONKEYS *Cercopithecus (nictitans)* group

OTHER NAMES Greater periphery monkeys. Fr. *Hocheurs*. Ger. *Fromm Meerkatze*. Swah. *Kima*.

MEASUREMENTS HB 310–590mm (♀), 410–700mm (♂). T 550–1,090mm. W 2.2–5.2kg (♀), 3.5–12.0kg (♂).

In terms of understanding the evolution of biota in African forested regions, this superspecies could be the single most important complex of regional populations in all of Africa. Further research is overdue and urgent.

RECOGNITION Large, long-tailed, arboreal monkeys with grizzled backs and crowns, black forearms, hands and feet, and dark tails. Coat patterns often have yellowish or reddish zones. Facial patterns are variable (see above). Adult males of all species make very loud and distinctive, explosive 'pyows'.

GEOGRAPHIC VARIATION Putty-nosed Monkey, *C. (n.) nictitans* (all drainage basins west and north-

Top, from left: Central African Putty-nosed Monkey, Pluto Monkey, Moloney's Monkey, Stuhlmann's Blue Monkey, Mount Kenya Sykes's Monkey.
Below, from left: Guinea Putty-nosed Monkey, Zaire Basin Gentle Monkey, Mbele Gentle Monkey, Silver Monkey, Tanganyika Sykes's Monkey.

west of Congo R.): dark species with white nose spot. Gentle Monkey, *C. (n.) mitis*: similar species without a nose spot. Diverse eastern forms are sometimes treated as a third species, *C. (n.) albogularis*. Likewise the Mbele Monkey, *opistoctictus*, might deserve to be treated as yet a fourth species group.

DISTRIBUTION The biogeographic name, 'greater periphery monkeys', describes the marginality of this species within the main forest blocks. The only forest guenons with a wide distribution in southern and East Africa, gentle monkeys are exceptionally adaptable with respect to altitude but appear to be constrained or excluded in many areas by the presence of other primates. Their diets overlap with those of drill-mangabeys and several guenon species, so competition with these monkeys may be a factor limiting their distribution (and sometimes vice-versa). Disease may be another.

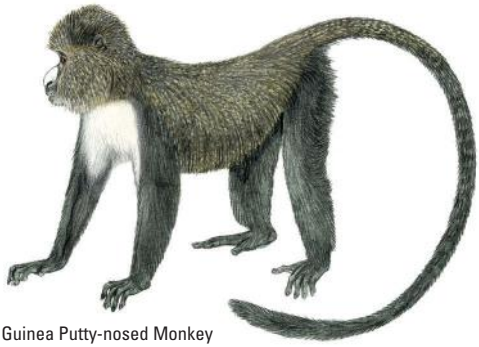
HABITAT Evergreen forests at various altitudes with a preference for well-shaded areas 10–20m from the ground. Gentle monkeys disperse easily along narrow riverine galleries which helps to explain why the pattern of distribution broadly corresponds with river basins.

FOOD Fruits and flowers (50–60%), leaf parts (20–25%) and invertebrates (10–20%). In many marginal areas a large proportion of the annual diet may come from relatively few species. While fruits remain the preferred food at all times, leaves and insects are taken during periods of shortage and an ability to digest leaves helps account for these monkeys' presence in areas where there are no other guenons. Animal foods tend to be sessile and are gathered by slow, intensive searching under bark and lichen.

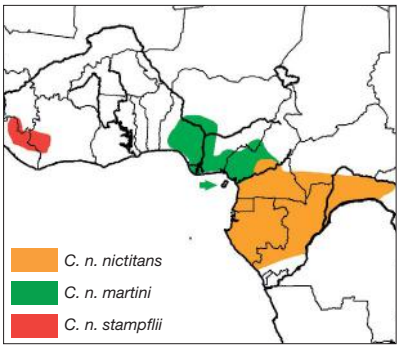
BEHAVIOUR Female groups with an average of between 10 and 12 breeding females and as many offspring are accompanied by a dominant male. While gentle monkey females exclude other females from the territory (very variable but may be about 60ha), the male is mainly concerned with keeping other males away from the females. Male 'tenures' in a territory vary greatly and may persist for only one or a few years before being displaced by one of the solitary males that often skirt around the peripheries of gentle monkey groups. Groups are also prone to frequent fissions and fusions.

ADAPTATIONS Gentle monkeys are generalised monkeys with two major adaptive advantages: first, they have highly developed arboreal skills (they are faster, more agile and better at negotiating all types of branches than either mangabeys or savanna monkeys); secondly, they are able to buffer long fruitless periods with foliage and insects. They would appear to be of optimum size for generalists but are too heavy to take full advantage of resources proffered on the more slender branches. This superspecies is excluded from consistently rich habitats where resources are efficiently partitioned among a suite of specialist primates. They are at a relative advantage in less rich, less stable forests where the specialists are unable to offset shortfalls of their staple foods.

STATUS Gentle monkeys are common over most of their very extensive range but are rare in Upper Guinea and the central Congo basin.



Guinea Putty-nosed Monkey
Cercopithecus (n.) nictitans stampflii



Putty-nosed Monkey

PUTTY-NOSED MONKEY *Cercopithecus (nictitans) nictitans*

OTHER NAMES Greater Spot-nosed Monkey. Fr. *Hocheur*. Ger. *Grosse Weissnase*.
MEASUREMENTS HB 400–530mm (♀), 420–570mm (♂). T 560–1,000mm. W 2.7–6.1kg (♀), 3.5–9.8kg (♂).
RECOGNITION A large, long-tailed, arboreal monkey with dark, grizzled olive fur on the back, crown, cheeks and base of the tail. The limbs and distal half of the tail are black or dark grey. A brilliant white nose spot in a dark face is this monkey's most striking peculiarity. Territorial males utter a very loud 'pyow' call.
GEOGRAPHIC VARIATION *C. n. nictitans* (Cameroon highlands and R. Sanaga east to Congo R. and south of R. Uele/Ubangi to about 23° E): dark greyish olive back and head, entire underside dark, laterally bunched fur on cheeks. *C. n. martini* (Bioko I. and S Nigeria): khaki-olive back and head, variable amounts of white and light grey on underside, throat off-white, chest dusky grey. *C. n. stampflii* (Upper Guinea): khaki-olive back and head, crown more vertically bunched and cheek-fur deflected downwards, chest and armpit area white.
DISTRIBUTION From Côte d'Ivoire to Guinea (but very sparsely and patchily). The contrast between Putty-nosed Monkeys' abundance in central West Africa and rarity west of the Dahomey Gap suggests they may have been recent and non-competitive colonists in habitats where the Lesser Spot-nosed Monkey (as well as diana monkeys, mangabeys and three colobus species) were, until recently, widespread and successful forest primates.
HABITAT All evergreen forests from lowland to montane, primary, secondary and narrow galleries and patches; not common in swamp or mangrove forests. Constraints from the plant community are less than those from competing primates.
FOOD Fruits, seeds, flowers, foliage and invertebrates. In Gabon the limiting effects of the male's larger size is evident in the fact that only 58% of its year-round diet consists of fruits while the figure is 76% in the case of females. Both sexes take a similar proportion of insects but males take a higher proportion of foliage (30% to the female's 12%). Caterpillars, ants and spiders make up the bulk of their invertebrate foods.
BEHAVIOUR Putty-nosed Monkeys live in groups of 12–30 females that defend a territory and are accompanied by a single adult male. Males utter booming rallying calls, 'pyows' and alarm hacks.
ADAPTATIONS The French name for this species, *Hocheur* or 'wagger', refers to a common appeasement gesture involving ritualised head-flagging, which gives prominence to the white nose. Their greetings sometimes combine the universal 'presenting' posture with head-flagging and lip-pouting (a combination that can involve comical contortions).
STATUS This species may benefit when human predation on primates is selective. Although *C (n.) nictitans stampflii* is now very rare in far West Africa, IUCN lists the species as a whole as of least concern.

GENTLE MONKEY *Cercopithecus (nictitans) mitis*

(for convenience includes *albogularis* and *opisthostictus*)

OTHER NAMES Diademed Monkey, Blue Monkey, Sykes's Monkey. Fr. *Cercopithèque à diadème*. Ger. *Diadem Meerkatze*. Swah. *Kima*.

MEASUREMENTS HB 310–590mm (♀), 410–700mm (♂). T 550–1,090mm. W 2.2.–5.2kg (♀), 3.5–12kg (♂).

RECOGNITION Large, long-tailed, arboreal monkeys very similar to the Putty-nosed Monkey but without its distinctive nose-patch. Back and thighs are grizzled while the forearms, hands, feet and terminal half of tail are black. The underside is relatively dark. The cheek-fur is also grizzled but the boundary with paler chin fur is very labile from one population to another. The bristly fur on the forehead forms a pale or grizzled brow-patch in some species but is undifferentiated in others. Longish muzzle in male.

GEOGRAPHIC VARIATION The arbitrary splitting of *mitis* into two geographic divisions (*mitis* and *albogularis*) obscures a more complex pattern of distribution among various subgroups. As with the *mona* group, differences in chromosome number have been found within the *nictitans*/*mitis* groups which may require a revision of existing classifications. In the meantime *C. mitis* can be divided into as many as six 'clusters' (each a potential species), and each embracing more than one subspecies.

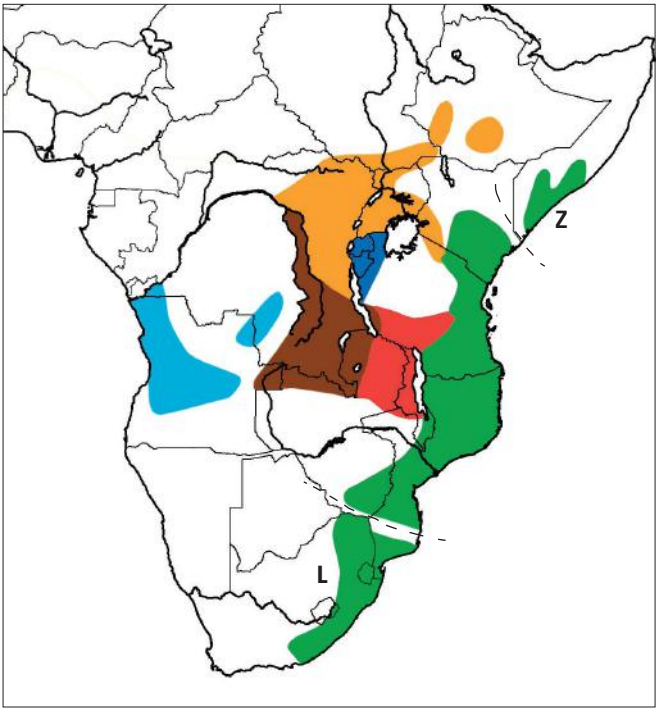
***Cercopithecus (n.) opisthostictus* cluster**

The Mbele Monkey cluster (*opisthostictus*, *heymansi*). Exceptionally soft, dense, light olive to steel-grey agouti body pelage, with long, drooping cheek-fur sometimes hiding ears. Restricted to low-lying, sometimes swampy forests. Probably the most conservative member of the *C. (nictitans)* complex. Has a chromosome count of 2n=70. Seems to co-exist with *C. (n) moloneyi* without interbreeding in a narrow region of overlap.

***Cercopithecus (n.) mitis* cluster**

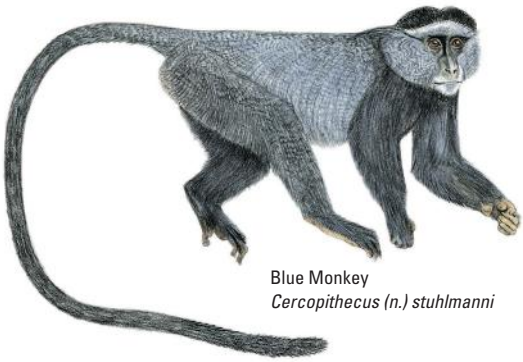
The Pluto Monkey cluster (*mitis*, *maesi*, *pluto*). Pale diadems and chin. Cheek-fur graduates from paler near face to darker on margins. Sporadically distributed on the western margins of Congo basin.

Gentle Monkey



opisthostictus cluster
mitis cluster
doggetti cluster
moloneyi cluster
stuhlmanni cluster
albogularis cluster
L *labiatus*
Z *zammaranoi*

Moloney's Monkey
Cercopithecus (n.) moloneyi



Blue Monkey
Cercopithecus (n.) stuhlmanni

White-throated or Sykes's Monkey
Cercopithecus (n.) albotorquatus

Golden Monkey
Cercopithecus (n.) kandti

***Cercopithecus (n.) doggetti* cluster**
The Silver Monkey cluster (*doggetti*, *kandti*, *schoutedeni*). Isolated populations associated with Western Rift Valley. Silver Monkey, *doggetti*, grizzled grey or golden back, black cap with sharply defined, grizzled diadem, high, rounded, grizzled cheek patches; Golden Monkey, *kandti*, is a high-altitude colonist on volcanic mountains near L. Kivu; Schouteden's Monkey, *schoutedeni*, a tiny population on Shushu I. in L. Kivu. All three show 'founder-effects'. Long muzzle in males.

***Cercopithecus (n.) moloneyi* cluster**
The Moloney's Monkey cluster (*moloneyi*, *francescae*). Montane areas of SW Tanzania, N Zambia and Malawi. Dark, grizzled backs, flat, dark caps with pallid diadems, pale chins, broad and low, grizzled cheek patches. Longish muzzle in males.

***Cercopithecus (n.) stuhlmanni* cluster**
The Blue Monkey cluster (*stuhlmanni*, *elgonis*, *boutourlinii*) – the latter an Ethiopian isolate, Expansive range in E DR Congo, Ethiopia and East Africa to Great Rift Valley from putative centre in Rwenzori Mts. Very dark, grizzled back, black cap with sharply defined blue-grey grizzled diadem, high, rounded, grizzled cheek patches. Relatively short muzzle in males.

***Cercopithecus (n.) albogularis* cluster**
The White-throated/Sykes's Monkey cluster (*albogularis*, *labiatus*, *erythrarchus*, *monoides*, *kibonotensis*, *kolbi*, *albotorquatus*, *phylax*, *zammaranoi*). Indian Ocean littoral distribution. Grizzled

back, grizzled cap and diadem not clearly differentiated. Populations from extreme outer margins of range, South Africa (*labiatus*) and Somalia (*zammaranoi*) are notably very dark coloured and possibly retain more features of earlier colonist ancestors. Boundary between white or pale chin fur and grizzled cheek fur very variable. Medium-sized muzzle in males. *C. a. zammaranoi* (Somalia) is a dwarfed, almost black form (HB 390–430mm) that is of special interest because another dwarfed population, also on the outer margins of the *C.* (*nictitans*) range, long ago likely gave rise to the *C. (cephus)* radiation.

HABITATS All types of evergreen forest from riverine, delta, gallery, secondary, primary and montane, including bamboo. Gentle Monkey densities within these habitats are variable.

FOOD Diet varies greatly by region and season and between the sexes (males eating less fruit). It is thought to be strongly influenced by the presence of other primates. Gentle Monkeys can tolerate quantities of leaves and stems in their diet but prefer fruits wherever possible. Sources are exploited for as long as they last and are often from trees that produce gluts of fruits. In some areas they rely on smaller, more active monkey species to lead them to fruiting trees. Insects form a regular and significant part of their diet and are gathered by slow, systematic searching through bark, lichen, moss and rotten wood.

BEHAVIOUR Social groups average 10 breeding females and their offspring accompanied by a single male. Numbers are subject to much local variation and fluctuation. Territories, averaging 60–70ha, are defended by all group members. The male's loud calls primarily advertise his association with a group of breeding females rather than being territorial. Loud calls are not regularly answered by other Gentle Monkeys but may evoke loud calling in Red-tailed Monkeys sharing the same home range.

ADAPTATIONS In their diet, behaviour and extensive range, Gentle Monkeys reveal themselves to be the most versatile and generalised of all arboreal forest monkeys. Numerous subspecies could be expected across so many latitudes and different forest types. However, the complexity of distribution patterns and variations in range and population densities suggest that fluctuating numbers and frequent isolation have been a consistent feature throughout their evolutionary history. They are too arboreal to compete successfully with semi-terrestrial savanna monkeys and too generalised for long-term success in a fully diversified primate community.

STATUS It is possible that relict groups in Ethiopia or in the L. Kivu area could become endangered but the species as a whole is not. In IUCN lists, local forms have been given different ratings.

CEPHUS MONKEYS *Cercopithecus (cephus)* group

OTHER NAMES Lesser periphery monkeys. Fr. *Cercopithèques du groupe cephus.* Ger. *Cephusmeerkatze.*

MEASUREMENTS HB 340–580mm. T 460–920mm. W 1.8–6.0kg.

Strictly speaking this very distinctive group is a subset within the *C. (nictitans*) Group.

RECOGNITION Long-tailed, arboreal monkeys with grizzled brownish backs and crowns and very diverse and brightly coloured face patterns. Tails are red in several populations and bicoloured in others. Typically very lively, active monkeys, they make jerky movements of the head and forequarters. Very staccato, chirping alarm calls are made by all species. Uttered in prolonged series by several or all members of a group, these volleys of sound are often a first indication of their presence.

GEOGRAPHIC VARIATION (see p.143 for facial patterns).

Lesser Spot-nosed Monkey, *C. (c.) petaurista* (NW Sierra Leone to Benin): bicoloured khaki/white tail, black face framed by a white ruff, white nose-spot.

White-throated Monkey, *C. (c.) erythrogaster* (SW Nigeria): bicoloured khaki/white tail, dark grey face, very attenuated grizzled cheek patches, broad and conspicuous white ruff framing the face, black or white nose, red or slate-grey belly.

Sclater's Monkey, *C. (c.) sclateri* (eastern margins of R. Niger delta): off-white tail, blue face, yellowish cheek-fur with sinuous border, pale muzzle.

Moustached Monkey, *C. (c.) cephus* (between R. Sanaga, Congo R. and R. Ubangi): red or bicoloured tail, bright blue face, broad yellow cheek-ruffs, black and white 'moustache'.

Red-eared Monkey (Red-nosed Monkey), *C. (c.) erythrotis* (between Cross R. and R. Sanaga): red tail, purplish face, cream cheek-ruff with linear black border, red nose and ears.

Red-tailed Monkey, *C. (c.) ascanius* (from Congo R. /R. Ubangi east to Uganda and W Kenya, S Sudan to Angola and N Zambia): partly or wholly red tail, dark blue face, white or grizzled cheeks and temporal region with variable margins, colour of nose-spot shows regional variation.

DISTRIBUTION Equatorial forests from Sierra Leone to W Kenya and about 10° latitude north and south. Absent from colder latitudes and higher altitudes, and from strongly seasonal forests of SE Africa.

HABITAT Lowland and medium-altitude forests with high temperatures and well-distributed rainfall. Cephus monkeys traverse a very wide range of branches, lianas and tangles at all but the very lowest levels of the forest. Individuals forage in a wide scatter, covering up to 1.5km per day in a territory of about 35ha. In Uganda (where members of the *mona* group are absent) densities of Red-tails can reach 140–175 animals per km^2. In Gabon, where cephus monkeys co-exist with Crowned Monkeys (in about equal numbers) and talapoins (locally much more numerous), they are estimated to live at less than a third of the density of Red-tailed Monkeys in Uganda.

FOOD Mainly whole fruits and seeds (but known to include many insect-infested samples). Cephus monkeys find and arrive at fruiting trees earlier than other species (often feeding at dawn) but are more readily displaced. When not feeding at super-abundant fruit sources they are persistent and thorough foragers for scattered fruits and insects. The nutritional value of a very varied insect diet is thought to be more significant than its average volume (about 20%). Leaves, buds and stems are taken as a temporary expedient. In east-central Africa this dietary buffer helps them inhabit a larger region and more habitat types than monkeys of the *mona* group.

BEHAVIOUR Groups of females with their offspring number 10–40 and are usually attended by a single male (occasionally more). Females defend their territory against other groups and even chase off solitary males. Territories often overlap those of gentle monkey groups (among which territorial males have similar but very much louder calls). Cephus monkeys frequently duet with resident gentle monkey males, apparently in order to augment their more feeble calls. As with most guenons there are pronounced seasonal peaks in breeding, with most births occurring between November and February.

ADAPTATIONS The *cephus* group is, in several respects, a neotenous (juvenilised) form of gentle monkey (*nictitans*). In addition to being smaller and having a more juvenile-looking skull these monkeys have a faster metabolism and are more active for a longer day than the gentle monkeys. They are also highly visually oriented and in polyspecific groups often warn other species of danger. This visual specialisation is corroborated by optical physiology (their eyes have more short-wave cones, which are especially sensitive to both space and colour perception). In contrast to gentle monkeys, which forage in groups for hidden insects, cephus monkeys are visual hunters that independently scan foliage and branches for exposed insects. This visual bias is clearly linked with greater use of visual signals. All species have evolved striking facial patterns which correlate with ritualised head-flagging displays performed during courtship and appeasement. Sharp head movements are also typical of this species and include contact and greeting gestures.

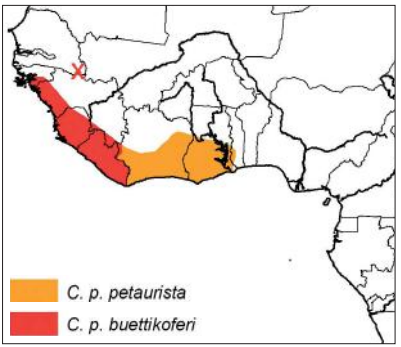
The diversity of facial patterns displayed within the *cephus* group suggests that this lineage must have become fragmented at an early stage in its evolution. Climate was clearly the isolating factor here. Lower temperatures and rainfall (during ice ages) would have affected this group more than others because insects and fruits would have become more seasonal over broad areas of central and West Africa. They would have been one of the first groups to come up against intensified competition for diminished or more seasonal resources.

In spite of their apparent diversity, all face patterns in this group are permutations and elaborations of a single facial format of the gentle monkey type. These patterns can be seen to arise through facial fur developing various pleats, deflections or tufts, through colour tinting of skin and fur, and through 'expansion' and 'contraction' of a limited number of dark or light patches (see figs on pp.142–3). The radiation of the *cephus* group is likely to have started in West Africa (*erythrogaster* and *petaurista* as modern derivatives) with an initial eastward expansion no further than the R. Ogooué basin (*cephus* and *sclateri* as modern derivatives) followed by a later further eastward expansion (*erythrotis* and *ascanius* as derivatives).

STATUS While the group as a whole is widespread and common, several species are rare or endangered.

LESSER SPOT-NOSED MONKEY

Cercopithecus (cephus) petaurista



Lesser Spot-nosed Monkey

OTHER NAMES Fr. *Hocheur à nez blanc.* Ger. *Kleine Weissnase.*

MEASUREMENTS HB 290–490mm (♀), 440–527mm (♂). T 570–787mm. W 2.3–3.8kg (♀), 3.9–5.0kg (♂).

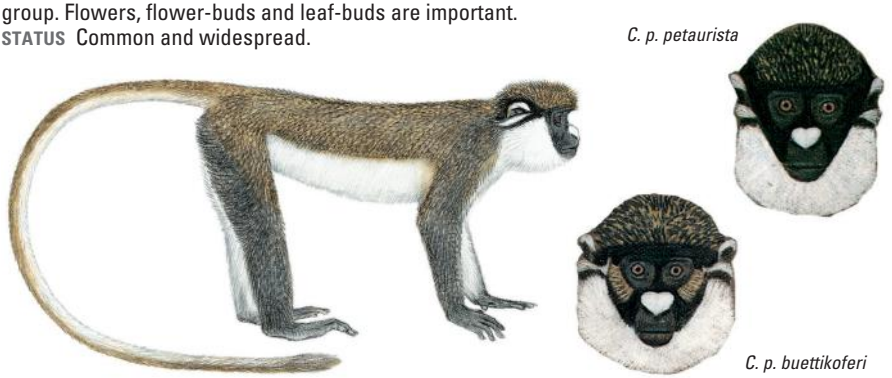
RECOGNITION Grizzled khaki-coloured back and crown, graduating to grizzled grey on outer limbs. Underparts, throat, ears and nose spot are white. The face is black and the tail is bicoloured. Adult males utter a peculiar grating hack and a high-pitched whistle of alarm.

GEOGRAPHIC VARIATION *C. p. petaurista* (Benin to R. Cavally): narrow black margins to orbits, white stripe only below ear (upper face). *C. p. buettikoferi* (R. Cavally westwards to Guinea): narrow cheek-patches of grizzled fawn on orbit margins, white stripe from temple to ear (lower face).

HABITAT Lowland primary and secondary forests, riverine and gallery forests, secondary regeneration and coastal bush.

FOOD This monkey is highly frugivorous and may eat fewer insects than other species in the *cephus* group. Flowers, flower-buds and leaf-buds are important.

STATUS Common and widespread.



WHITE-THROATED MONKEY *Cercopithecus (cephus) erythrogaster*

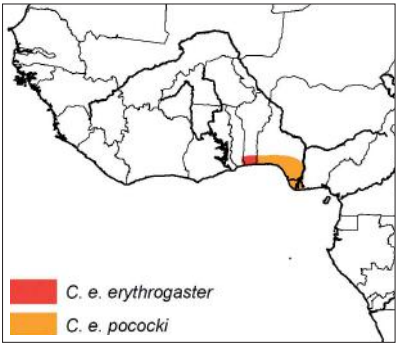
OTHER NAMES Red-bellied Monkey. Fr. *Cercopithèque à ventre rouge.* Ger. *Rotbauchmeerkatze.*

MEASUREMENTS HB 380–450mm (♀), 457mm (♂). T 580–700mm. W 2.4kg (♀), (est.) 3.5–4.5kg (♂).

RECOGNITION Grizzled khaki back, shoulders and thighs, dark grey outer limbs, lighter inner limbs and a bicoloured tail. The very prominent white ruff frames the dark face, which has narrow, grizzled cheek-patches. The cap is black with a broad triangle of pale grizzled fawn. The belly is grey or russet (the latter mostly towards the west of its range) and the nose is either black or white. The distinctive loud call of the male most resembles the grating hack of the Lesser Spot-nosed Monkey.

GEOGRAPHIC VARIATION Red-bellied Monkey *C. e. erythrogaster* (S Benin); White-throated Monkey *C. e. pococki* (SW Nigeria to Niger Delta).

HABITAT Widespread but very scattered in remaining lowland rainforests of SW Nigeria and S



White-throated Monkey

White-throated Monkey

Benin. Also in secondary bush and old farmland, usually in dense vegetation between 2 and 15m. Foraging parties number about five but groups of up to 30 have been recorded. At the heart of its remaining range a spacing of one group per km² has been estimated.

FOOD Fruits and insects.

STATUS All forests in SW Nigeria are subject to intensive logging, clearance and hunting. This species is currently unprotected but a 67km² wildlife sanctuary has been declared in the Okomu Forest Reserve. This species also occurs in the Ifon and Omo Forest Reserves. Listed as Class B (African Convention), Appendix II (CITES), endangered (IUCN).

SCLATER'S MONKEY

Cercopithecus (cephus) sclateri

OTHER NAMES Fr. *Moustac de Sclater*.
Ger. *Nigeria Blaumalkatze*.

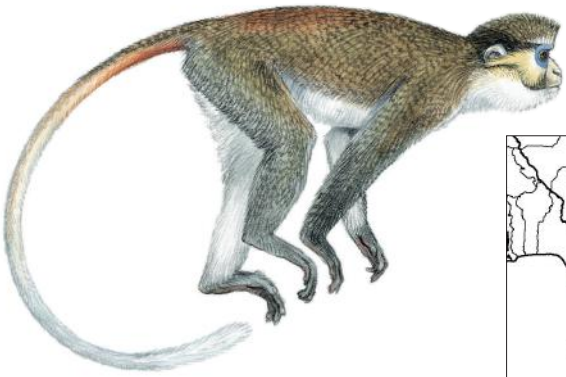
MEASUREMENTS HB 326–341mm (♀), 373–375mm (♂).
T 610–850m. W (est.) 3.1–4.6kg (♀), 5.0–5.5kg (♂).

RECOGNITION Grizzled olive-brownish back, shoulders and crown with a warm suffusion on the lower back. Outer surfaces of limbs are grizzled grey. The tail graduates from light olive to off-white, with a deep russet suffusion on the underside close to the anus: russet can spread over variable areas of the tail. The cap is peaked and encircled by a black margin. The facial skin is blue and there is yellowish cheek-fur, with a sinuous dark-tipped border above the white throat and chin-fur. Muzzle and ears are usually pallid but animals from towards the Cross R. valley have varying tints of red on the nose and ears.

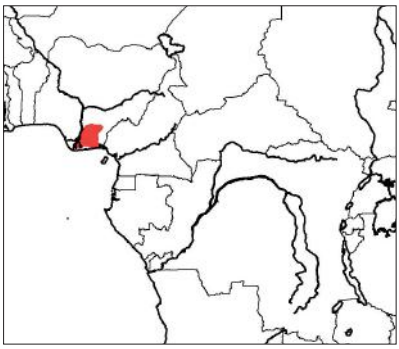
HABITAT Relict forests and swamps between the R. Niger delta and the Cross R. south of Enugu.

FOOD Likely to resemble that of other cephus monkeys: fresh foliage, fruit and invertebrates.

STATUS Putative hybrids with the Red-eared Guenon have led to it being classified with that species. Aside from this hybrid influence, the face pattern of Sclater's Monkey combines features characteristic of the western Lesser Spot-nosed and White-throated Monkey with



Sclater's Monkey



Sclater's Monkey

Distribution of the *cephus* group of monkeys in the central forest block. *Top left:* Sclater's Monkey *Cercopithecus sclateri* and the Red-eared Monkey *C. erythrotis*. *Top right:* a newly observed and as yet unnamed type, which may be a variant of the Yellow-nosed Red-tail *C. ascanius whitesidei* (*centre*). The Moustached Guenon *C. cephus* (*centre left*). *Far right:* Uganda Red-tail *C. ascanius schmidti*. *Below left:* Spectacled Red-tail *C. ascanius atrinasus* and Angola Red-tail *C. ascanius ascanius*. *Right:* Katanga Red-tail *C. ascanius katangae*.

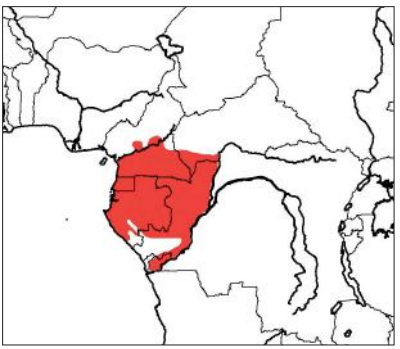
those of the more highly elaborate Moustached and Red-tailed Monkeys, suggesting that it is a conservative species illustrative of the common origins of the *cephus* group radiation as a whole.

A survey in 1988 recorded small populations in the R. Niger delta, notably within the AGIP oilfield west of Oguta, Imo State. In 1996 I pointed out that this was one of the rarest and most interesting monkeys in Africa and that oil companies had a responsibility to take practical steps towards its conservation. No such conservation measures have yet been initiated in the Delta region, an outstanding centre of rare endemic plants and animals. Currently listed as Class B (African Convention), Appendix II (CITES), classed by IUCN as vulnerable.

MOUSTACHED MONKEY

Cercopithecus (cephus) cephus

OTHER NAMES Fr. *Moustac*. Ger. *Blaumaulkatze*.
MEASUREMENTS HB 440–500mm (♀), 500–600mm (♂). T 660–990mm. W 1.8–3.8kg (♀), 2.6–5.2kg (♂).
RECOGNITION Back and crown are grizzled, with a light underside and red or grey tail. The facial skin is bright blue, with broad yellow cheek-ruffs and a vivid white 'moustache' of very variable shape above the jet-black lips and very bristly black fur at the corners of the mouth.
GEOGRAPHIC VARIATION *C. c. cephus* (R. Sanaga to Congo R. and R. Ubangi). *C. c. cephodes* (between R.



Moustached Monkey

Moustached Monkey

Ogooué and R. Kouilou): bicoloured grey tail). *C. c. ngottoensis* (R. Sangha to R. Lobaye).

HABITAT Lowland rainforest between the R. Sanaga and Congo R./R. Ubangi. Prefers dense foliage and liana tangles and will make use of all forest levels except the lowest. The distribution between Red-eared Monkey and Red-tailed Monkey (very similar forms) suggests that Moustached Monkeys may have recently expanded their range out of an Ogooué basin heartland.

FOOD Mainly fruits (and about 10% leaves, stems and shoots). Adult males have been found to eat much fewer insects than females, which suggests that social monitoring may be at the expense of time spent searching for insects. Often in polyspecific associations.

STATUS Formerly very common and widespread; listed as of least concern.

RED-EARED MONKEY

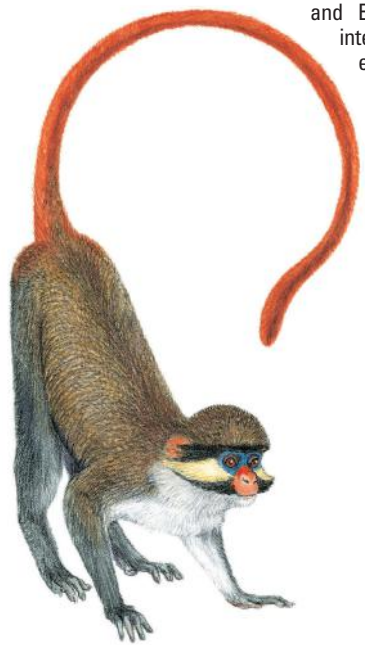
Cercopithecus (cephus) erythrotis

OTHER NAMES Red-nosed Monkey. Fr. *Moustac à oreilles rousses*. Ger. *Rotnase*.

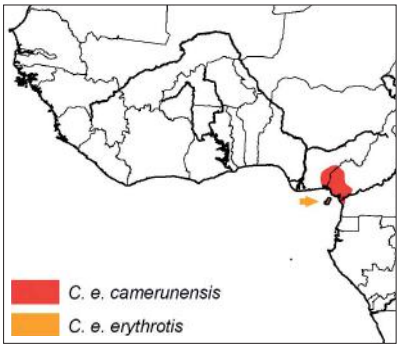
MEASUREMENTS HB 360–430mm (♀), 390–550mm (♂). T 460–770mm. W 2.25–3.5kg (♀), 3.0–5.6kg (♂).

RECOGNITION Grizzled brown back, shoulders and crown, red tail and rump, and grey forearms, hindlegs, hands and feet. Underparts and inner limbs are white. The face is purplish blue, with cream cheek-fur tapered to a point below the ear and with bold black margins. Nose and ears are red.

GEOGRAPHIC VARIATION *Cercopithecus e. erythrotis* (Bioko I.): smaller, darker island race. *C. e. camerunensis* (mainland population): larger, less melanic.



HABITAT Lowland rainforests between the R. Cross and R. Sanaga and Bioko I. Today the Moustached Monkey inhabits the intervening country between the very small range of the Red-eared Monkeys and that of the Yellow-nosed Red-tail (some specimens of which resemble it very closely). It seems likely that the range of the Red-eared Monkeys has contracted. Their ecological niche resembles that of other cephus monkeys but they are reported to live mainly in lower forest strata and in regenerating secondary forest. Putty-nosed and Mona Monkeys frequently follow and associate with Red-eared Monkeys.



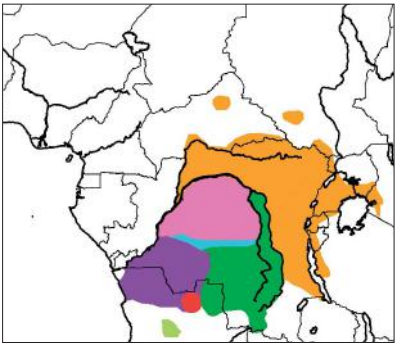
Red-eared Monkey

FOOD Fruits and insects.
STATUS Deforestation and plantations have destroyed a large part of this species' range and remaining populations are heavily hunted. Selection for extreme wariness may be taking place. It still survives in Korup NP Park and Douala Edea Reserve. Although it occurs in many smaller forest reserves it enjoys no practical protection and is in decline everywhere. Listed as Class B (African Convention), Appendix II (CITES), IUCN classes this species as vulnerable.

RED-TAILED MONKEY

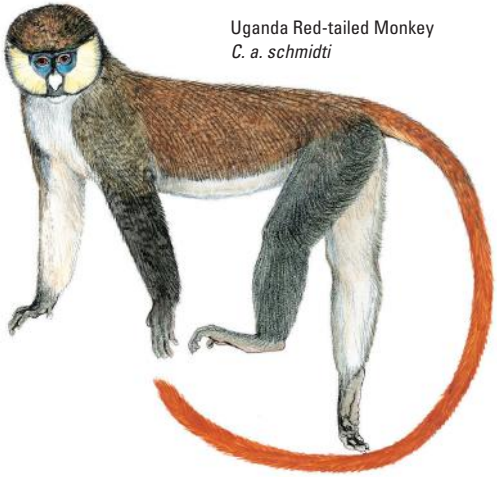
Cercopithecus (cephus) ascanius

OTHER NAMES Fr. *Cercopithèque ascagne*. Ger. *Kongo-weissnase*.
MEASUREMENTS HB 340–485mm (♀), 430–545mm (♂). T 670–920mm. W 1.8–4kg (♀), 2.2–4.9kg (♂).
RECOGNITION Grizzled brown back and crown, and grizzled grey outer limbs, hands and feet. The tail is partly or wholly red and the face is dark blue. Cheeks and temporal region are white or grizzled, with variable margins above the off-white throat and chin. The nose spot varies in colour and shape by region and subspecies.
GEOGRAPHIC VARIATION



Red-tailed Monkey

Angola Red-tailed Monkey, *Cercopithecus a. ascanius* (lower Congo R. and R. Kasai to R. Cuanza): broad black brow and temporal streaks, broad black boundary below white orbit-to-ear cow-licks, minuscule grizzled tawny patch below the orbits, blunt white nose-patch.
Katanga Red-tailed Monkey, *C. a. katangae* (from N Angola and south Congo basin to R. Lomani and R. Lualaba): black brow and temporal streaks, black boundary below white orbit-to-ear cow-licks, grizzled tawny patch below orbit, white nose-spot laterally elongated and tapering between nostrils.
Yellow-nosed Red-tailed Monkey, *C. a. whitesidei* (south of Congo R. to R. Kasai): narrow black temporal streaks and narrow black boundary below white orbit-to-ear cow-licks, variable grizzled tawny patch below orbits, T-shaped nose-patch varying from white to russet red, ears also white to red (see p.143).
Spectacled Red-tailed Monkey, *C. a. atrinasus* (Lunda plateau): very broad black brow and temporal streaks and very broad black boundary below white orbit-to-ear cow-licks, completely black muzzle and only a trace of grizzling in the black patch below bright blue orbits (see p.143).
Uganda Red-tailed Monkey, *C. a. schmidti* (from R. Ubangi north of Congo R. to Uganda and W Kenya, east of R. Lualaba to R. Lukuga): narrow black brow and temporal streaks, narrow black boundary around broad creamy-white cheek-ruffs, scalloped white nose-spot in narrow dark muzzle, blue facial skin (see p.143).


Uganda Red-tailed Monkey
C. a. schmidti

Intermediate forms occur along all open boundaries between these forms. Intermediates between Red-tailed and Moustached Monkeys are known from the R. Ubangi region.

With respect to face pattern, the Yellow-nosed Red-tail is conservative (some individuals resemble Red-eared Monkeys very closely) while the Uganda Red-tail is the most derived. This form appears to have expanded its range (both east and west) very recently.

HABITAT Lowland and submontane forests, riverine galleries and most stages of colonising, secondary or regenerating forest (except for those on poor soils). Red-tailed Monkeys also occur in forest mosaics with a high preponderance of single-stand species, such as ironwood.

FOOD Fruits make up half or more of the diet while insects make up a quarter. Flowers and flower-buds are also important. Leaves and leaf-buds become a significant part of the diet during seasons of shortage. The flowers of bean trees, *Markhamia* and panga-panga, *Millettia* (two common colonist trees) and the fruits of false nutmeg (*Pycnanthus*), false figs (*Trilepisium*) and red milkwood (*Mimusops*) are especially favoured and are stored in the cheek-pouches until the flesh and flavour have dissipated (a habit that ensures wide dispersal of the seeds). Feeding on fruits close to the sleeping-site begins at dawn (sometimes just before) and is often followed by displacement by larger monkeys. Except for the midday rest, the monkeys are often occupied hunting insects in the late morning and especially the afternoon. Feeding on fruits may then be resumed in the evening, as other monkeys retire, and continues up to nightfall. Major super-abundant food sources (especially those near the borders of two or more territories) may draw in temporary aggregations numbering more than 100 monkeys. Such groups are temporary and typically fraught with aggression.

BEHAVIOUR Females and their young form the stable core of Red-tailed Monkey society. Two or three reproducing females can eventually give rise to a group of 20 or more adult males, all with offspring. As numbers increase, the resources of a relatively small territory (mean size 35ha but over 100ha in forest mosaics) become scarcer. Because females do not normally leave their maternal group and oestrus tends to be synchronised (June–September), single attendant males become unable to deter invading females, especially during the oestrus peak. Multi-male groups are temporary and unstable. During feeding and especially while hunting insects, Red-tails typically disperse individually or in small family clusters. Antagonisms between clusters within large groups culminate in permanent fission, with new smaller groups setting out fresh territorial boundaries. Male 'tenancies' may last from a month to more than 6 years. In addition to fathering all offspring of the group the male is principal scout and sentry. He will also distract predators that threaten the group and his loud calls, threat coughs and branch-shaking help to demarcate the home-range.

STATUS Red-tailed Monkeys have been important subjects in the epidemiology of various viral diseases, including Yellow Fever. They have been used as laboratory animals and are a favourite exhibit in zoos. Widely treated as vermin.

Uganda Red-tailed Monkey *C. a. schmidti*

PROSIMIANS STREPSIRRHINI

Lorisids	Lorisidae
Galagos	Galagidae

The woolly-coated arboreal prosimians, with monkey-like hands and pointed, scent-sensitive noses, have been called both progressive insectivores and primitive primates. Their now time-honoured name (meaning 'monkey-forerunner') carries the unfortunate implication of animals frozen in a time-warp, while regrouping of the primates has saddled them with the even less fortunate name of Strepsirrhini, 'twist-nosed'. In reality they are distinctive and successful members of many modern ecological communities.

RECOGNITION There are two major groups of prosimians in Africa (with others in Asia and Madagascar). The galagos or bushbabies are arboreal walkers and leapers, with long tails, elongated hindlegs and relatively large ears. The potto group (lorisids) are arboreal clingers and climbers with very short tails, limbs of equal length and relatively short ears. Both groups are wholly nocturnal, have round heads, pointed muzzles, forward-facing eyes, a moist nose and a cleft, 'tied' upper lip. They are distinct from monkeys and other primates in the structure of their placenta, retina, inner ear, blood circulation and digestion. All species have modified lower incisors which form a fur-comb (in some species the incisors also form a sharp chisel). Hands, feet and fingernails have been modified in various minor ways but all have a spatulate, fur-grooming claw on the second digit of the foot. These specialisations, known to be very ancient, serve to keep the woolly fur in good condition. Fur is important as an insulator and as a scent-dispenser. Scent plays a major part in their social and territorial behaviour.

GENEALOGY/GEOGRAPHY It had long been thought that the pottos' closest relative might be the Asian Slow Loris. The angwantibos' nearest relative was thought to be the Asian Slender Loris, while the galagos were seen as a separate, uniquely African group. Recent molecular studies now indicate that all the African Lorisidae are more closely related to each other than to the Asian lorises. The remarkable similarities displayed between these distinct Asian and African groups suggest that the types of ecological niche available to nocturnal climbing primates are highly specific and so give rise to animals displaying similar physical characteristics.

Several galagos not only have close equivalents among Madagascan lemurs but also resemble some totally unrelated marsupials in Australia and South/Central America. Fruit-eating carnivores (olingos and kinkajous) in the South American rainforests also resemble lemurs in several respects. The New Guinea marsupial cus-cuses have several potto-like characteristics. Such resemblances across continents and orders suggest that the generalised body form typical of the earliest arboreal mammals has remained under tight constraints in small, nocturnal species, so that phylogenetically distant animals can look superficially very similar – convergent evolution.

ECOLOGY Fruit and animal foods are combined in different ratios by all prosimians. Few rely very heavily on fruits and this may be due to competition, not only from diurnal birds and mammals, but also from fruit bats, which are better adapted to seek out all major sources of ripe fruits. Most prosimians eat tree gums to a greater or lesser extent. These not only serve as a 'filler', permitting them to survive quite long periods of shortage, but may also provide them with scarce nutrients because prosimians appear to possess a special capacity to digest this low-energy resource. Buffered by gums, many prosimians are well-adapted gleaners of marginal resources (both fruit and animal) in the face of much competition. Although predominantly an equatorial forest group, a few galago species have adapted to acacia and other dry-country woodlands. Their dependence on forests and woodlands for food and shelter has precluded them from crossing the desertic barriers that confine them to Africa.

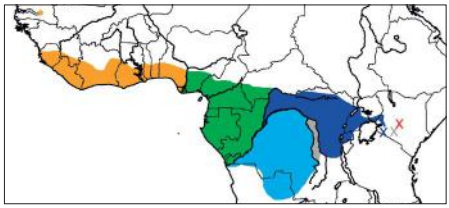
NATURAL HISTORY Prosimians are vulnerable to predation by carnivores, diurnal primates, owls and large reptiles.

ADAPTATIONS The individual profiles below describe various ways in which body sizes, limb proportions and minor anatomical structures of these otherwise generalised arboreal climbers and jumpers have been modified to perform various, more specialised functions.

LORISIDS LORISIDAE

Common Potto	*Periodicticus potto*
Martin's Potto	*Pseudopotto martini*
Angwantibos	*Arctocebus* (2 species)

COMMON POTTO *Perodicticus potto*



Common Potto

OTHER NAMES Fr. *Potto de Bosman*. Ger. *Potto. Swah*. Kami.

MEASUREMENTS HB 300–400mm. T 50–100mm. W 800–1,600g.

RECOGNITION A slow-climbing, woolly, arboreal animal with both hands and feet able to grip with exceptional power. The body and legs, disguised by thick brown fur or a hunched position, are actually long and slender. The head is round, with small, naked ears and protuberant golden-brown eyes. Hands have a rudimentary knob for an index finger. The neck joins the back of the skull and the entire region of the shoulders, the neck and crown of the head in presenting a compact mass of muscle, bone and very thick skin under dense fur. Near the centre of this apparent shield, elongated spines of 5–7 neck vertebrae, each enclosed in a densely enervated sleeve of skin, project from the surrounding tissues (but concealed in fur from which a clump of long easily detatched vibrissae may sprout). Apocrine secretions are concentrated in the genital regions of both sexes and large scent sacs under the 'pseudoscrotum' of females are known to excite and attract males. These glandular structures attest to the role of olfactory signals in the complex, but still little-known, socio-sexual lives of Common Pottos.

GEOGRAPHIC VARIATION *P. p. potto* (R. Niger to S Senegal), *P. p. edwardsi* (R. Niger to Congo R. and R. Ubangi), *P. p. faustus* (south of Congo R./R. Lualaba), *P. p. ibeanus* (R. Ubangi east to East African Rift Valley), *P. p. stockleyi* (Mt Kenya). Some of these taxa may eventually prove to be distinct species.

DISTRIBUTION Senegal to Kenya.

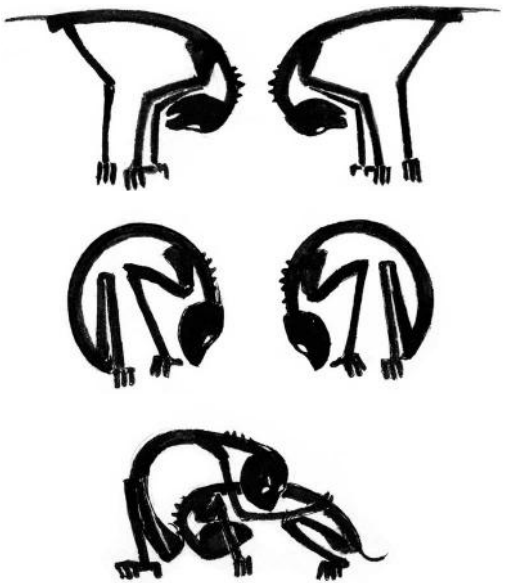
HABITAT Lowland, swamp and lower montane forests; commonest in seasonally flooded, secondary and colonising forests and along margins.

FOOD Distinct seasonal variation in more marginal zones where gums are dominant during drier periods, and insects, snails and fruits during the rains. Recorded fruits frequently include figs. Eggs and fungi, ants, caterpillars, beetles, larvae, spiders, slugs and snails are also eaten.

BEHAVIOUR Generally viewed as solitary (and therefore assumed to be so) Common Pottos are cautious and exceptionally silent animals that forage and mostly sleep on their own. Notwithstanding their apparently unsociability, recent studies have revealed that male and female individuals may consistently form durable pairs or a single male may sustain intensive links with up to three

females. Females range over 6–44ha while males have 9–40ha ranges. However, range areas are likely to vary greatly because densities of up to 28 individuals per km^2 have been recorded. Such high densities demand a complex social system and imply that inter-male competition should be significant – yet fights or signs of frequent wounding are rare. How potential male conflict over females might be mitigated is discussed under Adaptations. Both sexes scent- and urine-mark. When a female is in oestrus she makes a clicking want call that closely resembles the mother–infant contact call. Copulation can last up to 4 minutes. Gestation ranges from 194 to 205 days. Juvenile males leave their territory and wander widely. Juvenile females are accommodated by shifts in the mother's ranging pattern.

ADAPTATIONS Both males and females have large apocrine glands and patches of specialised glandular skin in the genital area and scent clearly plays a key role in socio-sexual behavior. Potto neck spines appear not only to stimulate the flow of secretion in the genital region of a partner but enervation of the skin covering the spines implies that their owner might also be rewarded by contact. Within any local Common Potto community it would seem that almost daily visits and the frequent exchange of individually differentiated scent secretions between each male and his one or more female partners serves to inform and generally deter other males. Furthermore males have been found to monitor their female partners regularly, spending some hours in the immediate vicinity of each female visited. Males may transfer their own genital secretion manually to anoint the back or neck of their partner, but pottos also hug one another in a fashion that brings the genital region of either sex into direct contact with their partner's neck. Here each partner can enjoy stimulation either of its genital area or of its super-sensitive neuchal spine skin. This mechanism for scent exchanges between the sexes is unique to Common Pottos as are ritualised inter-male contests. Such males trade short but powerful clashes with their shoulders, each contestant butting from a firmly clamped base.



Diagrams of main socio-sexual interaction between Common Pottos. Both sexes have richly ennervated and super-sensitive neuchal spines, skin and genitalia in these chemically complex areas. *Above:* Two males (occasionally females) butt neck/shoulders. *Middle:* Individuals confront passively. Potential for aggression or closer contact. *Below:* 'Hugging' in which genitalia and associated glands are stimulated by neuchal spines: behaviours and morphology that are still a challenge to science.

It is possible that the evolution of such extraordinary behaviours began with a slow, short-sighted primate, travelling through a maze of branches, needing to anticipate both hostile and amicable encounters with a quick defensive hunch. Pottos are so strong-wristed that one of their greatest advantages is resistance to being dislodged. After its initial shoulder-hunch, either sex can deliver a damaging canine slash to any enemy and it is this bite, rather than the ritualised shoulder-butt, that is the potto's last line of defence. That the neuchal spines have a primarily socio-sexual function (rather than an anti-predator role) is corroborated by the observation of a male and female engaging in shoulder-butting immediately before copulation. For each participant, the information that emerges from neck-to-neck clashing therefore seems capable of mediating both inter-male and inter-sexual relations.

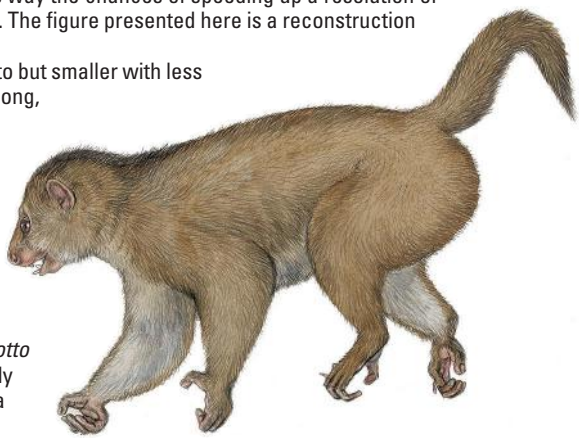
Common Pottos spend the day in dense tangles, hunched over a branch to which they cling. The limbs are served by vascular bundles that allow circulation to be maintained while the animal remains immobile for long periods.

STATUS Widespread and common.

MARTIN'S POTTO *Pseudopotto martini*

MEASUREMENTS HB (est.) 270–300mm. T (est.) 80–120mm. W (est.) 400–650g.
RECOGNITION The distinctness of this species has been rejected by some scientists who claim that its peculiarities are within the range of variation among Common Pottos. Indeed, it may turn out that such aberrant individuals of the Common Potto exist. However, it seems to me that the possible existence of a distinct species, perhaps genus, needs to be brought to the attention of field naturalists. In this way the chances of speeding up a resolution of this controversy may be increased. The figure presented here is a reconstruction (based on the type skeleton).

Said to resemble a Common Potto but smaller with less prominent muzzle and relatively long, tapered tail.



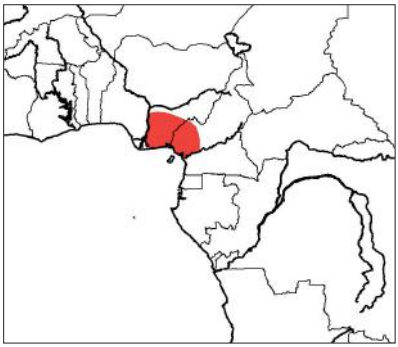
HABITAT Uncertain; possibly restricted to montane forests in the Cameroon highlands and, perhaps, to lower-lying forests in the immediate vicinity.
FOOD Its teeth imply a more insectivorous diet than the Common Potto.
BEHAVIOUR A supposed *Pseudopotto* has been seen to climb vertically when disturbed, and fled at quite a fast pace, in bursts of action.

ANGWANTIBOS *Arctocebus*

Calabar Angwantibo	*Arctocebus calabarensis*
Golden Angwantibo	*Arctocebus aureus*

CALABAR ANGWANTIBO *Arctocebus calabarensis*

OTHER NAMES Northern Golden Potto. Fr. *Potto de Calabar*. Ger. *Calabar Barenmaki*.
MEASUREMENTS HB 224–263mm. T (vestigial). W 230–465g.
RECOGNITION A small, almost tail-less, woolly climber with relatively short limbs (of even length), very slender wrists and tiny hands and feet. The rounded head has short, naked ears, large eyes and a pointed muzzle. This species differs from the Golden species in colour, minor teeth, skull and anatomical structures. It has soft, tan-brown upperparts and a white underside. In both species the hands, in which the second finger is lost and the third is reduced to a stump, are unique. Extremely sensitive to any disturbance, this species will quickly decamp to denser vegetation or freeze into a humped ball.
DISTRIBUTION Between the R. Niger and R. Sanaga within the lowland rainforest block but very patchy and localised.
HABITAT Confined to areas of very dense, low undergrowth with abundant lianas and vines within primary, secondary and coastal rainforest. The Calabar Angwantibo particularly favours the leafy growth that springs up in clearings, tree-falls and along forest edges. It sleeps hunched up on a branch in dense shade, well protected from sun and rain.
FOOD Mainly caterpillars, also beetles and fruits. Snails and small lizards have also been recorded.



Calabar Angwantibo

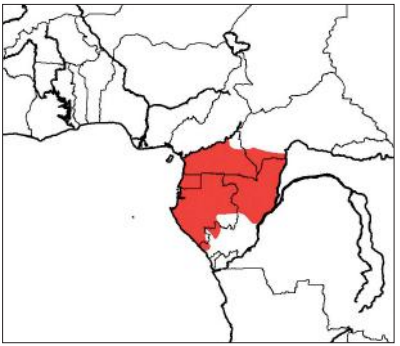
Caterpillars are found by smell in the course of carefully combing through liana tangles.

BEHAVIOUR Solitary; young accompany their mothers for some months after weaning, keeping in touch with a high-pitched clicking call. When caught or attacked they growl. Captive males when put together often fight, which suggests that they are territorial in the wild. After a gestation of just over 18 weeks the young are born well haired and with a strong clinging reflex. They are generally 'parked' by the mother as she hunts but they sometimes remain clinging to her body. The Calabar Angwantibo is able to produce two young in a year and will drive off an offspring on the birth of the next one.

Calabar Angwantibo

ADAPTATIONS The large eyes of this species appear to be primarily adapted to vision at extremely low light levels. The Calabar Angwantibo is most sensitive to sound and scent. It does not hunt by sight but sniffs continuously.

STATUS Normal census methods (walking through the forest with torches) are impossible for the Calabar Angwantibo because it hides its head and eyes at the least disturbance, depriving the observer of any clue to its presence. Wherever it is already established, small-scale clearances, selective tree-felling and road-making probably favour it. In such areas it is likely to become abundant in thickets and patches of dense secondary growth. Broader clearances, such as those made for plantations, clear-felling and agriculture, are likely to eliminate it because of the its weak capacity to disperse.



Golden Angwantibo

GOLDEN ANGWANTIBO

Arctocebus aureus

OTHER NAMES Southern Golden Potto. Fr. *Potto doré*. Ger. *Goldenbärenmaki*.

MEASUREMENTS HB 220–260mm. T (vestigial). W 200–270g.

RECOGNITION Small, woolly climber with a golden or russet-tinted upperside and creamy underside. Fine guard hairs on the back, shoulders and haunches have glistening, crinkled tips, which give a 'frosted', form-dissolving appearance to the hunched body. The pointed nose projects beyond the undershot jaws; the nostrils, sculpted and mobile, sniff continuously. Naked ears are less capable of free rotation than those of galagos and are more horizontally aligned. The fur is somewhat shorter than in the Calabar species and there are differences in the proportions of the teeth.

DISTRIBUTION Widespread all over the R. Sanaga to Congo R./R. Ubangi area but very localised and patchy.

HABITAT Confined to vine tangles and areas with abundant young (or slow-growing) leafy stems in moist evergreen, lowland rainforests. Large vertical branches are never climbed because the small, narrow hands and feet of this species are adapted only to close around stems less

than 6cm in diameter (the Golden Angwantibo never climbs spread-eagled with splayed palms). This angwantibo is very sensitive to heat, and continuous urine-marking also makes it extremely susceptible to dehydration so that it will die very quickly if exposed to the sun or if kept without water. It is absent from all markedly seasonal areas.

FOOD Caterpillars of all species, including hairy and distasteful species that are avoided by other insect-predators. Some of these caterpillars are colonial and many are abundant, especially on rank growth in clearings and on forest edges. The prey is discovered by scent (probably augmented by listening for sounds of the larvae chewing and excreting). Small caterpillars are grabbed and eaten whole, larger ones are held down and torn apart piecemeal, while hairy ones are thoroughly worked with the hands and savaged before being consumed.

The Golden Angwantibo avoids climbing higher than 15m (it mostly lives below 5m) due to heightened competition from birds, less consistent insect resources, more exposure to wind, sun and predators, and fewer thin-branched tangles to shelter in. It frequently descends to the forest floor for fallen fruits and invertebrates.

BEHAVIOUR Visits to the ground expose the Golden Angwantibo to predation and its defensive reaction is unique. The animal stands on widely spaced, rigid and fully extended limbs. The head is tucked well back on the chest. This elevates the hindquarters, which become the obvious focus for attack. If touched, however, the animal lunges at its attacker from between its legs with a very quick, slashing bite (it has very sharp canines). If on a secure site, the animal simply hunches into a ball. In any exposed situation it prefers to climb rapidly up to the nearest clump of dense foliage. Exclusively nocturnal, the animal's activity begins in the evening with a lengthy grooming session. Young animals that are 'parked' by their mothers progress from very limited movement within their 'parking lot' to more extensive explorations as they get older.

ADAPTATIONS Food, territory and socio-sexual relations are all mediated by scent. Both sexes leave urine trails over the branches on which they travel. Both sexes also have genital glands that produce copious secretions. Captive females have been seen to mark other females with scent while males also mark females. In the latter case the scrotum may contribute scents that may deter other males or condition the female to accept the male's advances.

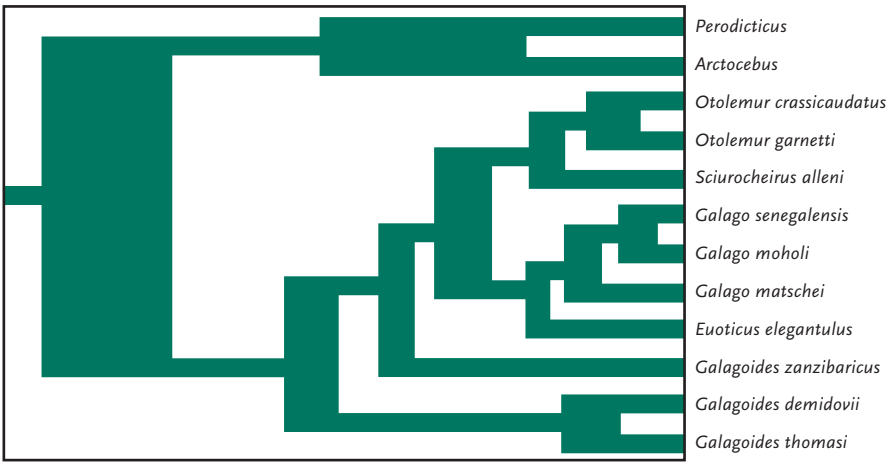
STATUS This species is protected by law in Gabon but is too small and too cryptic to face much danger from human predation. Clear-felling and large-scale clearances are a major threat to their habitat. The long-term safety of this species is of concern, mainly because of its biological uniqueness and relatively restricted range.

GALAGOS OR BUSHBABIES GALAGIDAE

Dwarf galagos	*Galagoides* (7 species)
Squirrel galagos	*Sciurocheirus* (3 species)
Greater galagos	*Otolemur* (2 species)
Needle-clawed galagos	*Euoticus* (2 species)
Lesser galagos	*Galago* (4 species)

RECOGNITION Long-tailed, woolly, nocturnal primates with long hindlegs and elongated bases to the feet (tarsi). The head is rounded, with forward-facing eyes and large, naked ears which can retract into compact, folded structures. The moist nose is at the end of a pointed muzzle. The neck is very flexible. Lower incisors are modified to form comb-like structures, and a toothed pseudo-tongue, which serves as a specialised 'comb' cleaner, is situated between the tongue and the floor of the mouth. Hands and feet have five long digits with spatulate, padded tips. Genital glands are strongly scented in both sexes. The saliva, the lips and the chest are also scented in some species. Head-and-body lengths range from 100 to 450mm (W 60–2,000g). The baby-like cries of the largest (*Otolemur*) have given galagos their common name but each species has one or more loud calls. Many species are best identified by such vocalisations, which differ more than their relative sizes or colours.

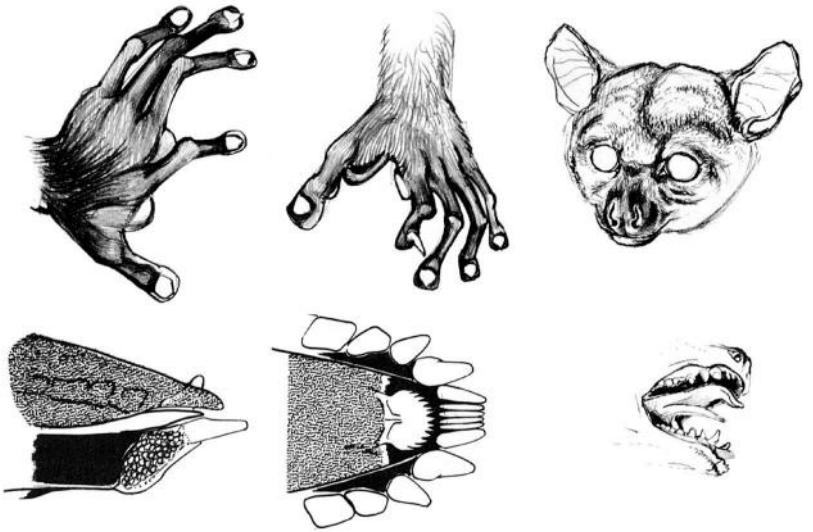
GENEALOGY Galagos have been a distinctively African lineage for an unknown period of time but were already well differentiated by 20 mya. Recently a large team, initiated by Dr Simon Bearder, has examined galagos across six fields of research including: (a) molecular studies; (b) anatomical re-examination – notably penile structures; (c) behaviour – especially recorded vocalisations;



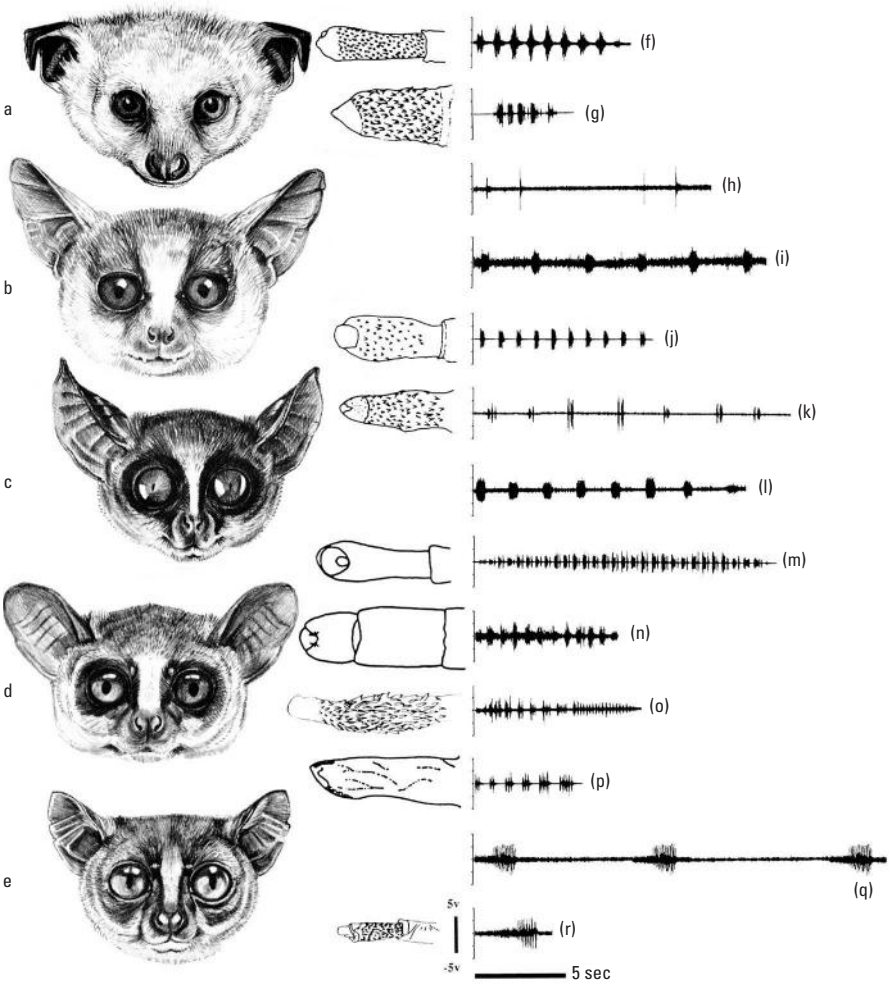
Tentative phylogenetic tree for the African lorisoids Lorisoidea (after Masters *et al.* 2007).

(d) ecology – especially locomotory patterns and life-zones; (e) biogeography – notably new forms from newly surveyed areas, revised estimates of natural variation within populations and revised assessments of distribution limits; (f) taxonomic revision – notably redefinition of generic characteristics and correction of mistakes in allocation of names. These studies have revolutionised our understanding of the biology and evolution of this extremely difficult group.

Differentiation clearly began quite early on and has given rise to dwarf 'running' forms, small 'frog-jumping' forms, greater galagos, needle-clawed gum-gatherers and lesser galagos. All lines of evidence suggest that forest-dwelling *Galagoides* species are the most conservative and the open woodland-adapted *Galago* species, the most derived (see phylogenetic tree above). The most recent, but still provisional, taxonomy lists five genera and 18 species.



Above left and centre: Spectacled Galago hand and foot. *Above right:* Small-eared Galago. *Below:* three views of tongue denticle and procumbent incisors displaying how the denticle fits under the tongue.



Faces, penile shapes and oscillograms of loud calls for some galagos.
(Courtesy of S. Bearder, M.J. Anderson and P. Honess.)
(a) Greater Galago. (b) Southern Galago. (c) Spectacled Galago. (d) Zanzibar Galago. (e) Thomas's Galago.
(f) Greater Galago. (g) Small-eared Galago. (h) Pallid Galago. (i) Allen's Galago. (j) Senegal Galago.
(k) Southern Galago. (l) Spectacled Galago. (m) Rondo Galago. (n) Matundu Galago. (o) Zanzibar Galago.
(p) Mozambique Galago. (q) Thomas's Galago. (r) Demidoff's Galago.

GEOGRAPHY Primarily an equatorial forest group that eventually extended into dry, seasonal woodlands in S and NE Africa. Although several morphological types range very widely, recent research has confirmed that these break down into regional or relict populations that are now regarded as species. They seem to have evolved distinct structures and unique vocal (and probably olfactory) communication signals that inhibit interbreeding.

ECOLOGY A need for secure diurnal refuges and extreme vulnerability to predators (notably eagle-owls, carnivores and nest-raiding primates) helps to explain their confinement to woodlands and forests in sub-Saharan Africa.

A link with gummiferous, widespread, often dominant leguminous trees is striking in several species. Reliance on gum as a major dietary item or as a famine-food is a partial explanation but

galagos may also have adapted in more subtle ways to the ecology of leguminous communities (perhaps to the growth form of trees and lianas and a specific insect fauna).

Some species have relict distributions, others have diverged by habitat and region. Multiple rainforest species co-exist by eating different foods, moving along different arboreal pathways by different locomotor patterns and embracing different life-zones. All species forage singly.

NATURAL HISTORY Matriarchal groups are the stable units in galago society, with a family defending a territory within which more mature females have preferred home ranges. Such preferences provide the basis for a slow turnover of female territories. Males are more intensely competitive and transitory, with single, very energetic and intolerant males travelling over 1–5 female territories every night. Subordinate males pass through stages of behaving like juveniles within the dominant male's range, becoming nomadic, and setting up small home-ranges on the peripheries of a dominant male's range.

Territories are advertised by loud calls and by laying down scent. Scent is laid indirectly, by urination into the palms of the hands and feet or by releasing urine directly onto the branch (and in some species by rubbing saliva or secretions from genital or chest glands onto branches). Males monitor females very frequently. Several species make nests; others sleep in hollow trees. The more social species utter rallying calls before dawn.

Oestrous lasts for about two nights and excites continuous and persistent interest from the males. After a gestation of 100–150 days the young are born in a nest or hollow. Rainforest species tend to give birth to a single young once a year, while woodland species frequently give birth to twins twice a year (higher reproductive rates in woodland species probably reflect higher levels of predation). The eyes of newborn galagos are half-open at birth but movements are weak and uncoordinated. At first the young are left in the nest but they later travel with, or on, their mother. Family members exchange scent by rubbing and grooming one another. Scrotal glands, salivary scents and apocrine lip glands all play a part in the regulation of social relations. Contacts between individuals vary from frequent to almost continuous in high-density habitats (where galagos can number 500 individuals per km^2). Scent is the most important social signal among galagos and, together with sound and touch, renders visual signals much less important, which helps explain why galagos resemble each other so closely.

ADAPTATIONS Galago fur is not only adapted to insulate the animal but also serves very effectively to hold and diffuse a range of scents secreted by the animal's various scent glands. Mutual- and self-grooming serves to bond individuals and to keep the scent-dispensing fur in prime condition, hence the complex modification of teeth and tongue structures, grooming claws and scented skin (not to mention saliva) as a grooming array. Eventually it should be possible to identify and classify galago species with reference to their distinctive scents, sounds and penis shapes. Simple visual identification of these nocturnal animals has its limitations but the development of photo traps has greatly assisted identification.

The limbs of some galagos are the mammalian equivalent of those of tree frogs. Both frog and galago can move from absolute stasis on one spot to a distant, unpredictable second point and then on to a third, within seconds. The success of frogs world-wide is an indication of how difficult it is for predators to beat this mode of locomotion. The vertical clinging and leaping skills of the galagos are also well adapted to movement within stands of well-spaced, narrow, vertical stems. This form of vegetation is commonly found under well-shaded forest canopies. The elongated upper foot, or tarsus, gives the galago great versatility of gait because rapid and wide flexion at the heel allows the animal to run fast with minimal involvement of the specialised thighs and shanks. It also helps the animal to accommodate to a variety of different landing sites (most acrobatically among thorns). Long tails provide balance and a rudder for changing direction while leaping.

Heavily obstructed and densely shaded undergrowth not only demands specialised locomotion, olfaction and big, light-gathering eyes, but also favours sound as a mode of communication and involvement of hearing in hunting for active prey. All galagos therefore have large ears that resemble those of bats in their mobility and great sensitivity.

DWARF GALAGOS *Galagoides*

Demidoff's Galago

RECOGNITION Diminutive galagos with greenish grey-brown coats, yellowish underparts and elongated, upturned noses. Until about 1980 all dwarf galagos were regularly classified as a single species because they all display similar body forms and coloration. As part of an ongoing, intensive reexamination of all galagos by Dr Bearder and his team, new species and newly recognised distinctions have emerged and are summarised here. Seven species are now recognised. These fall into four subgroups that cluster by anatomical and biogeographic characteristics but principally by voice – thus:

Crescendo callers: The smallest (Demidoff's or Dwarf Galago) and its closely related ally (Thomas's Galago) are distinguished by their relatively small hands and rising 'crescendo' loud calls. Widely distributed, equatorial and successful species. Recent genetic studies suggest that these two species derive from the very earliest stages of the galago radiation.

Scaling caller: Another very small species, *G. orinus*, known from montane, 'Eastern Arc' forests with a double or triple unit 'scaling' call.

Incremental callers: Slightly larger galagos, *G. cocos*, *G. granti*, more widely distributed in East African (mainly coastal) forests. Best identified by their 'incremental' calls.

Roller callers: Two small galagos, *G. rondoensis* and *G. zanzibaricus*, with long, spatulate fingers. Sparsely distributed in relict coastal lowland and piedmont forests in East Africa. Called 'roller callers' on account of their rolling loud calls. Recent genetic research suggests that *G. zanzibaricus* occupies an intermediate position in between other *Galagoides* and the rest of the galago radiation.

GEOGRAPHY Although found in cool highlands and coastal localities as far south as 28° S, these very small-bodied animals are mainly restricted to equatorial lowlands from Guinea to the Indian Ocean.

ECOLOGY Primary and secondary forests including very fragmentary relict outliers in East and south-east Africa. They are mainly insectivorous and although many take fruits most rely on gums as a seasonal stop-gap and 'filler'. Beetles, caterpillars, crickets and termites are known common prey.

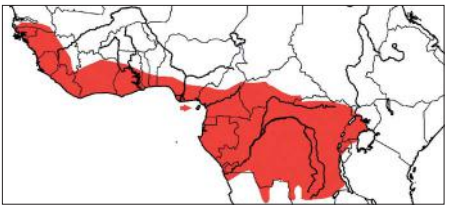
NATURAL HISTORY The preferred foods of dwarf galagos are exploited by small birds by day and by bats (notably slit-faced bats) at night. The galagos are commonly killed by owls and genets. Predation and competition are likely to confine them to tangled evergreen vegetation and limit their capacity to colonise new areas or disperse through exposed vegetation.

ADAPTATIONS Members of this group are primarily quadrupedal, making short leaps rather than long hops, but there are species-specific styles of locomotion. Dense evergreen thickets and forests in the tropics are primary habitats for dwarf galagos.

CRESCENDO CALLERS (EQUATORIAL DWARF GALAGOS)

Demidoff's Galago	*Galagoides demidoff*
Thomas's Galago	*Galagoides thomasi*

Equatorial dwarf galagos lack obvious visual characteristics so successful identification of a particular species is mainly dependent on vocalisations (for which a recorder is an essential tool). Among 'crescendo callers' only two species are currently recognised but regional populations are still poorly known. The tiny Demidoff's Galago lives at low levels while the marginally larger, more active Thomas's Galago is a canopy-dweller (wherever it co-exists with Demidoff's).



Demidoff's Galago

DEMIDOFF'S GALAGO *Galagoides demidoff*

OTHER NAMES Fr. *Galago de Demidoff*. Ger. *Urwaldgalago*.
MEASUREMENTS HB 120mm (73–155mm). T 180mm (110–215mm). Ear (ave.) 24mm. W 60g (44–97g).

RECOGNITION The smallest primate in Africa. The body colour is brown with paler yellowish underparts. Ears are relatively short and the nose is pointed and upturned, with a prominent white stripe between the eyes and down the bridge of the nose. Loud calls are very distinctive; a series of sharp chips that gather in speed and pitch to reach a crescendo in 2–4-second bouts. They also make an insect-like buzzing alarm call.

GEOGRAPHIC VARIATION *G. d. demidoff* (Senegal to R. Niger), *G. d. murinus* (R. Niger to Congo R.), G. *d. anomurus* (north of Congo R.), *G. d. phasma* (south of Congo R.), *G. d. poensis* (Bioko I.).

DISTRIBUTION Equatorial west and central Africa. Less certainly north and south of Lake Victoria.

HABITAT A strong preference for dense secondary growth on forest margins, in tree-fall (chablis) zones or along road margins (where densities of more than 100 animals per km^2 have been recorded in Gabon). Demidoff's Galagos may gather in sleeping parties of up to 10 animals, huddling in dense tangles of vegetation or in rudimentary leaf nests. They live mostly within 5m of the ground.

FOOD Mainly beetles, moths, caterpillars and crickets. During the dry season gum may be eaten but only accounts for a small proportion of the year-round diet. Fruits are also eaten sporadically and may account for up to 20% of the diet. Except for a lull at about midnight, galagos forage all night and alone but utter periodic contact calls.

BEHAVIOUR Living in overlapping home ranges of about 1ha, related females often sleep in huddles with neighbours and their offspring. Male home ranges of up to 2.7ha overlap those of several females of which one or more are monitored every night. Gestation lasts 110–114 days and new mothers avoid contact with other galagos for a week or more after giving birth. One or, less frequently, two young are born at a time. They are weaned by 2 months and are of adult size by 6 months. They can live for more than 12 years.

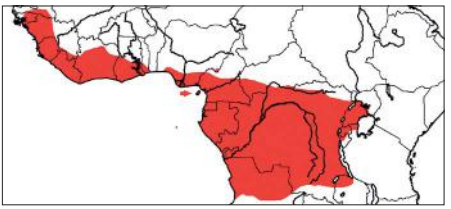
ADAPTATIONS Demidoff's Galagos occupy a micro-habitat occupied in similar fashion during the day by rope squirrels (*Funisciurus*). The density of the vegetation is such that it seldom necessitates long jumps and the small, deft hands and feet of the galagos are clearly best adapted to 'running' along very fine and more or less horizontal supports.

STATUS Common and widespread.

THOMAS'S GALAGO

Galagoides thomasi

OTHER NAMES Fr. *Galago de Thomas*. Ger. *Thomas galago*. Swah. *Komba Tomasi*.
MEASUREMENTS HB 140mm (123–166mm). T 260mm (150–240mm). Ear (ave.) 27mm. W 100g (55–149g).



Thomas's Galago

Thomas's Galago

RECOGNITION A small forest galago closely resembling Demidoff's Galago (until recently classed as a race of Demidoff's). The body is ashy brown with paler underparts. Fur colour is influenced by the individually variable production of yellow secretion from the skin. The face is generally paler than that of Demidoff's, the ears are somewhat larger and there are prominent eye-mask patches. The call is a repetitive, shrill, rasping chink which increases in pitch and speed and lasts about 4 seconds. It also makes a scolding chitter reminiscent of an epauletted fruit bat (*Epomophorus*) but is not known to utter buzz calls (as Demidoff's do).

GEOGRAPHIC VARIATION *G. t. thomasi* (E DR Congo, W Uganda), *G. t. subsp. nov.* (R. Niger to Congo R.). Distinct populations (probably new subspecies or even species) occur on the Loanda plateau in Angola, in the Shaba region of S DR Congo and possibly on Mt Marsabit in Kenya and in Togo. Central Ugandan animals are larger than those in W Uganda and have shorter tails. The West African animals differ in the pattern of their loud calls.

DISTRIBUTION Because this species has generally been lumped together with Demidoff's there is much uncertainty about its overall range. Now thought to range from Senegal and Angola to Kenya and Zambia in primary and secondary as well as seasonally dry forest.

HABITAT A high-canopy species in primary forest in the regions shared with Demidoff's Galago. Where Demidoff's is absent, as is the case in much of Uganda, Thomas's Galago appears to expand its niche. In central Uganda it is found in undergrowth and in secondary forests. It is more prone to climb up and down and jump between vertical supports than *G. demidoff*. It also inhabits higher, drier and more marginal forests.

FOOD Mainly insects, beetles, caterpillars, ants and termites, with some fruits and gum.

BEHAVIOUR Thomas's Galagos are thought to form localised social populations that may have little or no contact with neighbouring groups. Within an interacting group of about 12, sexes appear to be evenly balanced but the males comprise dominant 'breeders', subordinates and peripherals. Their nests are made daily or are augmented with fresh leaves cut each morning. In Uganda they may be made at any level and the leaves cut from many tree or forest grass species. Wet-season nests (often lodged in multiple forks) tend to be larger and are used longer than dry-season nests. This is unlikely to be influenced by breeding patterns because some young are born throughout the year, although there is a pronounced peak in December–February. The newborn are heavy-headed and poorly coordinated but development is very rapid. The mother can make long jumps with the baby in her mouth but by 2 weeks the youngster can accompany the mother away from the nest. By the age of 1 month it urine-marks, runs about and makes clumsy jumps. Weaned at 6 weeks, it is finding food of its own by 2 months. Strongly hierarchical relations between members of a local group may be mediated chemically. Bright yellow secretions emanating from bare skin on the face, ears, hands, feet and naked 'heel-spots' flow most copiously from the younger males and from females and their young just as they emerge from a semi-retired lactation period.

Thomas's Galago

An important difference between this species and Demidoff's is its greater skill at hopping and moving through more open (and often more vertical) growth.

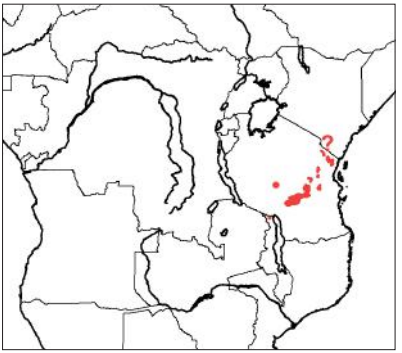
STATUS Common in appropriate localities.

SCALING CALLER (MONTANE DWARF GALAGO)

Usambara Galago *Galagoides orinus*

The voice of this species was recently shown to belong to a galago first described from the Uluguru Mts, in 1936, then classified as *Galago demidoff orinus*. It is now clear that this represents a distinct species.

USAMBARA GALAGO *Galagoides orinus*



Usambara Galago

Fr. *Galago uriner*. Ger. *Berggalago*. Swa. *Komba ya mlima*.

MEASUREMENTS HB 125–138mm. T. 169–199mm. E. 25–32mm. W. 74–98g.

RECOGNITION A distinctive loud advertising call described as a double or triple unit scaling call first recorded at Amani in the Usambara Mts but since recorded from the Ulugurus, Udzungwas and Mt Rungwe. Other distinctive vocalisations are a yapping alarm call and a series of descending screeches. A small, dark-brown galago with paler underside. Above the sharply pointed nose a narrow white nasal stripe contrasts strongly with dark brown and black surrounds to the eyes. Chin is yellowish white and the inner ear linings are conspicuously yellow in younger individuals (probably from skin gland secretions). The tail is very dark brown and evenly bushy. Field naturalists should be alerted to the presence of this species in Eastern Arc montane forests and be encouraged to investigate further, notably with the aid of recording devices and digital cameras.

The furthest limits of this species distribution await definition but it is possible that it occupies all montane areas between the Taita Hills in Kenya, along the Eastern Arc and southern highlands to highlands close to L. Malawi (L. Nyasa) (possibly on both sides of the lake).

This species makes globular nests of leaves and twigs, well concealed within dense growth, and nests may hold several animals. Bouts of calling are typically just before dawn and shortly after dusk. Agitated alarm calls against potential predators (owls, genets, people) can be sustained for up to an hour.

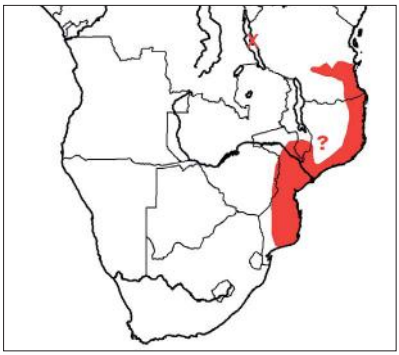
FOOD Gum (recorded from *Toddalia* vines), nectar (of wild banana), invertebrates and small vertebrates.

STATUS Presently not thought to be threatened, but felling of forests for commercial potato farms, and other crops, continues to erode its habitat in many mountain areas of Tanzania.

INCREMENTAL CALLERS (EAST COAST DWARF GALAGOS)

Mozambique Galago *Galagoides granti*
Diani Galago *Galagoides cocos*

Calls consist of a series of staccato notes, uttered in bursts lasting 6–10 seconds, with brief crescendos near the beginning or end. Unlike the relictual east coast galagos, these species seem to have wide geographic ranges (although they remain restricted to forested or riverine environments, coastal thickets and cultivation mosaics). There are at least two well-defined species (with a possible third in Malawi).



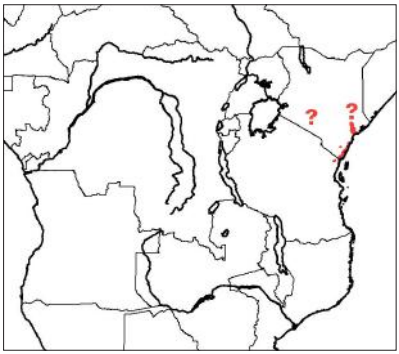
Mozambique Galago

MOZAMBIQUE GALAGO *Galagoides granti*

OTHER NAMES Grant's Dwarf Galago. Fr. *Galago du Mozambique.* Ger. *Mosambik-Galago.*
MEASUREMENTS HB 155mm (140–254mm). T 220mm (200–235mm). W 110–178g.
RECOGNITION The soft-brown body colour is suffused with ochre on the shoulders, back and thighs. Yellowish brown extends down the tail, the terminal third of which becomes very dark. The head is greyish with black-brown eye-patches and a broad interocular stripe of white fur. The forward-facing cups of the very rounded ears are pinkish white with black margins; these circular patterns have a strong visual impact and presumably act as intra-specific signals. Surface brushing of yellow sometimes suffuses the pale off-white fur of the underparts. Overall the fur is longer and woollier than in the Zanzibar Galago.
HABITAT Forest mosaics, riverine strips and coastal forests extending along the East African coast between the R. Rufiji and the R. Limpopo. The Mozambique Galago also extends inland up the valleys of the Zambezi and Rufiji watersheds.
FOOD Insects and fruits.
STATUS Widespread and common.

DIANI GALAGO *Galagoides cocos*

OTHER NAMES Kenya Coast Dwarf Galago. Fr. *Galago de Diani.* Ger. *Dianigalago.* Swah. *Komba ya Diani.*
MEASUREMENTS HB 158mm (142–183)mm. T 212mm (182–230)mm. E 23-40mm. W 117–172g.
RECOGNITION Brown body, limbs and tail (but distally near-black) with greyish-white underparts and inner surfaces of limbs. Orbital mask prominent with short white inter-orbital stripe. Ears are inconspicuous and tend to be carried more horizontally than in *G. granti* and are unlikely to have much visual signalling function.
HABITAT Coastal forests of Kenya and extreme NE Tanzania. These typically grow as low canopy, dense understorey communities (typically *Sterculia, Combretum, Tamarindus, Fagara, Zizyphus, Grewia* and *Ficus*) growing on fast-draining sands and coral rag. Shelters during the day in tree hollows where one or two females and their young may huddle with a male.
STATUS A very localised species but IUCN rate of least concern.



Diani Galago

Diani Galago

ROLLER CALLERS (EAST COAST DWARF GALAGOS)

Rondo Galago *Galagoides rondoensis*
Zanzibar Galago *Galagoides zanzibaricus*

This newly designated group embraces two species that were once classified as subspecies of Demidoff's Galago. First suspected to be distinct on the basis of recordings of their stereotyped loud calls. When captured, their identification as distinct new species was confirmed. The smaller of these new species comes from the far south of coastal Tanzania. The larger comes from Zanzibar, neighbouring coastal areas and some piedmont forests inland.

RONDO GALAGO *Galagoides rondoensis*

OTHER NAMES Fr. *Galago de Rondo.* Ger. *Rondo-galago.* Swah. *Komba ya Rondo.*

MEASUREMENTS HB 130mm (100–137mm). T 170mm. W 69g (60–73g).

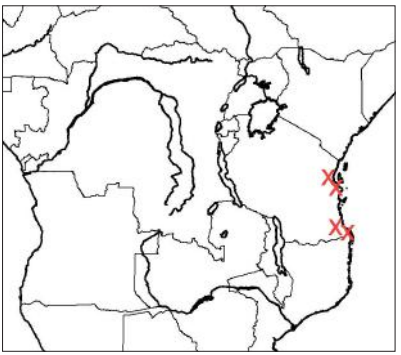
RECOGNITION A very small galago of warm-brown body colour, with a long, dark reddish-brown tail which becomes thicker towards its tip. The pale underside has yellowish tints. The nose is long, pointed and strikingly retroussé with a pale centre line between broad black-brown eye-patches. The main vocalisation is rather insect-like: a sustained vibrating call that rises in volume and is sustained for about 10 seconds before tailing off quite suddenly.

HABITAT Known from remnant forest patches on the moist seaward sides of low hills close to the Tanzania (and, perhaps north Mozambique) coast. Notably found in liana tangles that persist after tree-felling. Initially known only from Rondo plateau.

FOOD Insects, often pounced on from above. Like several bird species, these galagos attend army ant columns to catch fleeing invertebrates.

BEHAVIOUR Mainly leaping from vertical stem to stem, they can also cross open ground by hopping on the hindlegs.

STATUS Past logging of the Rondo plateau was almost total. Its known habitat and other neighbouring areas continue to suffer from relentless pit-sawing and frequent fires. IUCN lists this species as critically endangered.



Rondo Galago

ZANZIBAR GALAGO

Galagoides zanzibaricus

OTHER NAMES Fr. *Galago de Zanzibar*. Ger. *Zanzibargalago*. Swah. *Komba ya Zanzibar*.

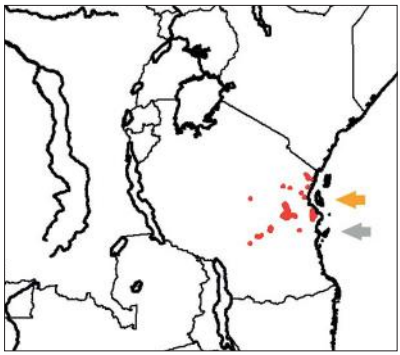
MEASUREMENTS HB 153mm (120–165mm). T 200mm (170–230mm). W 145g (104–203g).

RECOGNITION The dark-brown body colour is suffused with warm reddish tints on the crown, shoulders, back and thighs. The tail is ashy brown with hairs of very even length. The nose is pointed but less so than in other dwarf galagos and the lower jaw is shallow and long.

GEOGRAPHIC VARIATION

G. z. zanzibaricus (Zanzibar I.): cinnamon brown back, greyish crown, white nasal stripe between well-defined black 'mask' around eyes. Tail evenly haired, dark grey-brown. Underparts off-white, sometimes yellowish. Ears are well rounded.

G. z. udzungwensis (a scatter of lowland and piedmont forests in eastern Tanzania): greenish-brown body colour, with a long, somewhat graduated, dark brown tail. The ground colour graduates over the forehead into poorly defined sepia markings around the eyes. The lighter underparts show an orange flush, especially on the chest. It has a large but rather narrow head. Broad ears slightly 'pinched' towards their tips. Fingers and thumbs are exceptionally long and thin, with spatulate tips.



Zanzibar Galago

DISTRIBUTION Between R. Tana and R. Rufiji and Zanzibar I, also Mafia I.

HABITAT Coastal lowland rainforests and thickets, riverine forests and secondary growth, including cultivation mosaics and gardens, where it normally remains below 5m.

FOOD Invertebrates, mainly insects (moths and beetles) and up to 30% fruits. Gum is readily taken by captive specimens.

BEHAVIOUR Individual home-ranges of about 2–5ha may be wholly or partially shared with close relatives but females are intolerant of other neighbouring females. Single adult males associate with one or more females, sleeping by preference in leaf-lined tree holes. Gestation lasts 120 days and normally results in a single young. May breed twice a year (February–March and September–October). The young reach adult size in 4 months and are sexually active by 1 year. Up to 150 galagos per km^2 have been recorded in suitable habitats.

Matundu Galago
G. z. udzungwensis

Zanzibar Galago
G. z. zanzibaricus

ADAPTATIONS The Zanzibar galago is primarily an agile, arboreal 'runner' which also makes substantial leaps but never hops bipedally, nor can it land feet first. It can 'reverse-climb' backwards down vertical and near-vertical stems.

STATUS The Zanzibar Galago remains locally common in spite of continuous attrition of its habitats which are being cleared for cultivation. Proposed conservation areas on Zanzibar I. should ensure the preservation of viable populations there if protection is effectively enacted.

SQUIRREL GALAGOS *Sciurocheirus*

Allen's Squirrel Galago	*Sciurocheirus alleni*
Gabon Squirrel Galago	*Sciurocheirus gabonensis*
Makandé Squirrel Galago	*Sciurocheirus makandensis*

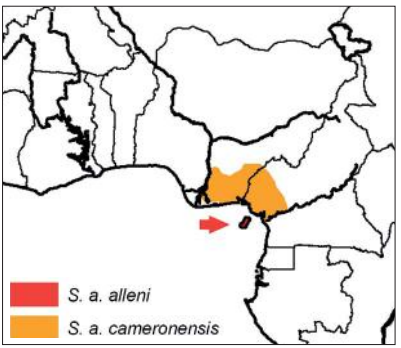
RECOGNITION Grey-brown or dark-grey galagos with various tints of russet to their limbs. Pointed muzzles have pale medial stripes and reddish eyes are set within well-defined mask patches. Squirrel galagos have carried frog-like vertical clinging and leaping to its extreme. They differ from most other galagos in landing 'hands first' or with all limbs simultaneously.
GENEALOGY Squirrel galagos are a distinct group but genetically most resemble greater galagos.
GEOGRAPHY Currently only known from between the R. Niger and Congo R., an area with the most consistently high rainfall in Africa.
ECOLOGY Almost entirely ground-feeders in primary forest with a heavily shaded relatively clear floor and numerous, well-spaced lianas and tree stems. Squirrel galagos avoid all areas of dense undergrowth and are effectively absent from secondary forest. Within this habitat, densities of 14–25 animals per km^2 have been estimated. Fallen and low-level fruits account for the greater part of the diet, with the balance made up of animal foods (beetles, moths, spiders, snails and frogs). The galagos pounce on hopping or flying insects with great precision, grabbing them in the hand.
NATURAL HISTORY Animals live in large territories with females ranging over 8–16ha and males over 30–50ha. Territorial males are very energetic in defending their mating rights over up to eight females, visiting as many as five in a single night. Rendezvous are facilitated by loud croaks to which others respond (a quieter croak serves to keep mothers and their offspring in touch). Animals scent-mark. Normally shelter in hollow trees, sometimes shared with bats or anomalures. Within such hollows may build rudimentary leaf-nests, especially when giving birth. Gestation is 133 days and one (rarely two) infants are born at a time. Two females and their offspring may sometimes share a shelter.
ADAPTATIONS Fallen fruits and attendant invertebrates are major forest resources for which there is much competition. The forest floor beneath fruiting trees provides foci of activity that attract predators, and the squirrel galagos' extreme alertness and instantaneous flight responses reflect increased vulnerability. However, their frog-like escape technique depends upon the forest floor being relatively unobstructed, with adequate fine-stemmed verticals to leap onto. It is possible that a squirrel galago exists in Côte d'Ivoire.

Allen's Squirrel Galago

ALLEN'S SQUIRREL GALAGO

Sciurocheirus alleni

OTHER NAMES Fr. *Galago d'Allen*.
Ger. *Buschwaldgalago*.
MEASUREMENTS *S. a. alleni* HB 230mm (200–290mm). T 270mm (220–300mm). W 400g (300–455g).
S. a. cameronensis HB 220mm (165–226mm). T 263mm (248–298mm). W 276g (220–355g).
RECOGNITION The mainland form of Allen's Galago is much smaller than the nominate Bioko I. form. Individual variations include near absence of the dark eye-mask and much variation in the degree of reddish or orangey tints on the outer forearms. The tail is long, bushy and of even thickness. All forms make long, distinctive whistles.



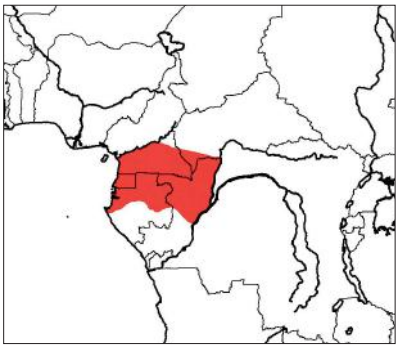
Allen's Squirrel Galago

GEOGRAPHIC VARIATION *S. a. alleni* (Bioko I.): very dark-brown island form. *S. a. cameronensis* (between R. Niger and R. Sanaga): small, head and body with grey-brown back, rump, crown and hindlegs, raw sienna limbs and grey-brown tail; voice a whistle and 'kwok'.
HABITAT Found between R. Niger and R. Sanaga where it lives in the lowest levels of mature primary forest.
FOOD Mainly fruits but insects also important.
STATUS The felling of primary forest destroys the habitat of this species. *S. a. alleni* listed as endangered (but IUCN rates species as least concern).

GABON SQUIRREL GALAGO

Sciurocheirus gabonensis

OTHER NAMES Fr. *Galago ecuriel du Gabon*. Ger. *Gabun-Buschwaldgalago*.
MEASUREMENTS HB 200mm (185–205mm). T 255mm (230–280mm). W 260g (188–340g).
RECOGNITION A medium-sized galago with off-white to grey underparts, sometimes with a red streak in mid-ventrum. Brown back, variable extents of orange or red tints on thighs, flanks and outer surface of arms, greyish crown and dark-brown to slate-grey tail. Voice a deep croak and short, rapid whistles.
HABITAT Lowland and piedmont forests between R. Sanaga and R. Ogooué. Eastern limits likely Congo R. and R. Ubangui.
FOOD Mainly fruit (73%) and small animal prey (25%).
STATUS Of least concern.



Gabon Squirrel Galago

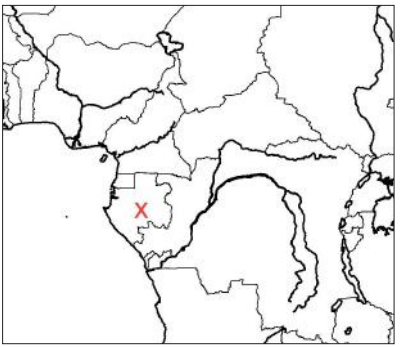
Gabon Squirrel Galago

Makandé Squirrel Galago

MAKANDÉ SQUIRREL GALAGO *Sciurocheirus makandensis*

OTHER NAMES Fr. *Galago ecuriel de la Makande*. Ger. *Makande-Buschwaldgalago*.
MEASUREMENTS Not yet measured. HB (est.) 220mm. T (est.) 260mm. W (est.) 400g
RECOGNITION A somewhat melanic sibling species to *S. gabonensis*. Very dark slate-grey back and tail, bold black eye-masks with outer limb surfaces mahogany and underparts dull pinkish

or orangey. Most distinctive calls consist of an alarm call that starts with a loud, two-part whistle followed by up to four whistles in declining pulses.
HABITAT To date only recorded from Forêt des Abeilles but probably ranges intermittently between the R. Ogooué and Congo R.
FOOD Fruit and invertebrates, the latter sometimes found near army ant swarms or snatched from them on procession.
STATUS On the assumption of a relatively wide range, of least concern. However, logging of their habitat continues at an accelerating pace.



Makandé Squirrel Galago

GREATER GALAGOS *Otolemur*

Greater Galago	*Otolemur crassicaudatus*
Small-eared Galago	*Otolemur garnetti*

RECOGNITION Cat-sized, long-tailed, woolly, arboreal animals of relatively uniform brown, grey or sandy colouring. Melanistic (black) morphs are common in some areas; the tail is sometimes of a paler tint. These are the largest and among the most primitive of living galagos. They lack strong colour contrasts on the body and face. The snout is broad and dog-like, and the eyes are proportionately smaller than those of any other galagos. The ears are prominent and ribbed. Greater galagos have glands on their heels, which are horny and rough.

More often heard than seen, the galagos' loud call begins as an explosive pulsing bawl or croaking which then tails off. Alarm calls (yapping, rattling or moaning cries) are often sustained for a long time.
GENEALOGY Greater galagos generally move on all fours and resort to springing leaps only when alarmed or in order to get from one tree to another. Although true galagos, their more generalised gait and less specialised limb structure is indicative of an ancient common ancestry shared by pottos and galagos.
GEOGRAPHY Range across the southern part of the continent from Angola and Namibia to the east coast from Natal to Somalia. The larger part of this extensive range is in miombo (*Brachystegia*) fire-climax woodland but within the more severely degraded or grassy areas of the miombo belt they are confined to riverine galleries and isolated thickets. Particularly numerous along coastal plains and on the lower slopes of mountains, they live in areas with well-defined seasons. There is virtually no overlap of range with pottos, nor are they found north of pottos' range.
ECOLOGY Greater galagos live at very variable densities strung out along river courses in the drier, more open savannas but continuously in coastal thickets and forests, where they have been estimated to number up to 125 per km^2. Home-ranges probably vary greatly but a tagged female was found to live within 7ha while a male was estimated to use around 20ha.

Many greater galago habitats are impoverished florally, with long dry seasons in which their main diet consists of tree exudates. When plants are fruiting and flowering, fruits and blossoms make up the main element in their diets. Invertebrates and (in some areas) vertebrates play a lesser role, although juveniles may prefer animal foods even when fruits and gum are available. Feeding tends to be spasmodic and animals may form temporary clusters during rest periods before breaking off to seek food again.
NATURAL HISTORY Ranges are shared and defended by related females. Dominant males also permit a small number of subordinate males within their ranges during the dry (non-breeding) season. Subordinate and peripheral individuals rely on scent-marks and loud calls to avoid face-to-face meetings with dominant animals; juveniles may accompany their mothers to form small groups.

The onset of the breeding season is marked by male gargling and clucking and by physiological changes in both sexes. Females only invite copulation while they are briefly in season, but mating is phlegmatic and may go on for hours. Gestation lasts 18 weeks. The female gives birth on a leaf-nest or platform and up to three young remain there for about 2 weeks, after which the mother carries

them with her in her mouth or on her back. By 25 days they are following her wherever she goes, only becoming wholly independent by about 300 days, at which time they tend to leave the parental range. Births peak in September on the East African coast and November in South Africa.

ADAPTATIONS Greater galagos have bare glandular patches on their abdomen and chest (larger in males) with which they mark favourite sites. These function as landmarks along their regularly used arboreal pathways. The oily yellowish apocrine secretion has three components, of which one dissipates in about an hour while the other two remain for several days. Other galagos smell scent-markings carefully and modify their movements in relation to both olfactory and vocal signals. In this way potentially dangerous confrontations are generally avoided. Chest-gland marking is often augmented by urine-marking and ano-genital deposits. The animal sparingly urinates on its hands and feet which it then rubs on the branch. Callosities on the palms of the feet grate on the bark, thus adding a sound signal to which other animals also pay attention. Foot-grating is also likely to spread secretions from the heel-glands which, in combination with the urine-marking, probably helps identify individuals. In these ways quite dense nocturnal traffic within shared home-ranges can be regulated.

GREATER GALAGO *Otolemur crassicaudatus*

OTHER NAMES Thick-tailed Galago, Large-eared Galago, Silver Galago. Fr. *Galago à queue épaisse*. Ger. *Riesengalago*. Swah. *Komba kubwa*.

MEASUREMENTS HB 320mm (260–465mm). T 410mm (290–550mm). W 1,100g (567–2,000g).

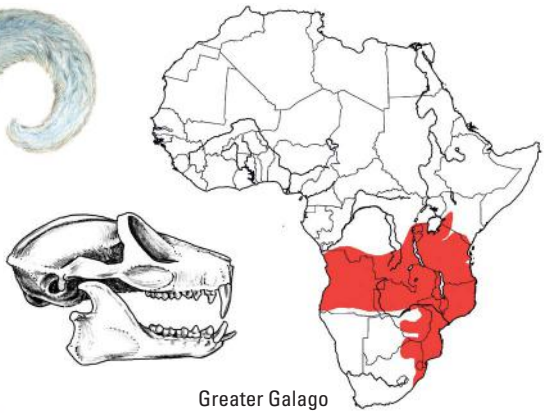
RECOGNITION A large, brown or grey galago with exceptionally long ears (50–72mm), a broad muzzle, large canines and relatively small eyes. There is a dense covering of long guard hairs on the lower back. There are scent-producing glands on the chest. The Greater Galago walks and runs in preference to leaping but can clear substantial gaps in the canopy.

GEOGRAPHIC VARIATION

O. c. crassicaudatus (south of R. Limpopo): brownish with tail less than 400mm long.

O. c. montieri (Angola to Tanzania): greyish with long tail and large ears.

O. c. argentatus (NE Tanzania and Kenya in riverine and other woodlands and lower montane forest to S and E of Kavirondo Gulf): large galago, silvery grey (sometimes black) with a very pale tail. The face is long and broad muzzled. Ears are generally less than 60mm.



Greater Galago

melanistic Greater Galago
O. c. argentatus

Mwera Galago (from photograph)

O. c. kirkii (Rufiji R. to Limpopo R.): greyish body, with brown extremities. A dwarfed form of *O. crassicaudatus* (with identical vocal repertoire) has been observed and photographed in Mwera, SE Tanzania within the range of *O. c. kirkii*. This 'Mwera Galago' is distinguished by its small size and by a pale brown, slender tail.

HABITAT Dense vegetation within various types of woodlands and savannas, notably along riverine strips and in orchards or gardens, even in relatively open, dry country where acacia and other gummiferous trees may be a significant attraction. They make habitual use of arboreal pathways, presumably guided by scent and memory. Locally and patchily common in miombo (*Brachystegia*), coastal and montane areas ranging up to 2,000m. This is the common Greater Bushbaby of southern and East Africa.

FOOD Acacia gums, flowers and seeds; figs, ebony and other fruits; snails, slugs, insects, reptiles and birds. Ratios of fruit, gum and animal prey vary with locality, season and with age, for example young, accompanied by their mother, may consume snails and insects while the adult only takes gum, seeds and fruit.

NATURAL HISTORY Females maintain exclusive territories while males have much larger ranges that overlap with numerous other males. Most frequently encountered as solitaires but mother–young groups, of up to two generations, may remain together for a year or more, sometimes to be joined by one, rarely more, adult males. Such groupings are only possible where food resources are locally abundant and concentrated.

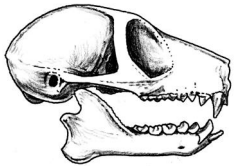
ADAPTATIONS Extremely vocal, these appear to be the most social of all galagos. Mutual grooming and amicable chasing are unusual features of this species. Entirely nocturnal, arboreal and quadrupedal. Capable of spread-eagled jumps, sometimes unfolding all limbs from a tense crouch into a fast spring that resembles that of a frog. Females give birth to up to three young and shelter neonates in cupped nests. These are constructed from leaves and vines manipulated by hands and teeth and hidden within dense tangles.

STATUS Common and widespread.

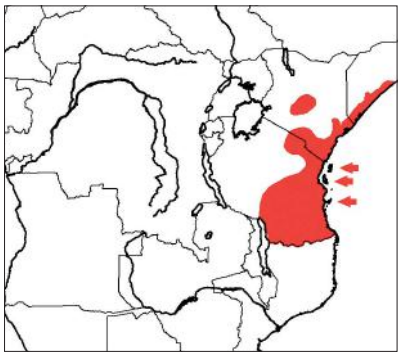
SMALL-EARED GALAGO *Otolemur garnettii*

OTHER NAMES Garnett's Galago/Bushbaby. Fr. *Galago de Garnett*. Ger. *Garnettgalago*. Swah. *Komba mkubwa ya Pwani*.

MEASUREMENTS HB 266mm (230–340mm). T 360mm (300–440mm). W 767g (550–1,040g).



RECOGNITION A medium-sized galago with relatively short ears, a pointed muzzle and relatively large eyes. This species was once



Small-eared Galago

treated as a subspecies of *O. crassicaudatus*. Convex fingernails. Active leapers. (Chromosomes and penile structure are distinctive.)

GEOGRAPHIC VARIATION

O. g. garnettii (Zanzibar, Pemba and Mafia Islands): uniform brown with dark or light tip to dark brown tail. *O. g. kikuyensis* (Kenya highlands mainly east of Gregory Rift): grey with brownish tail. *O. g. panganiensis* (N Tanzanian montane forests and R. Pangani south to R. Rovuma): greeny-grey-brown. *O. c. lasiotis* (East African coast north of Pangani): very variable colouring.

HABITAT Coastal and montane forests (often dry, low-canopy and florally impoverished) but also riverine galleries with numerous acacia trees; also various cultivation mosaics and urban suburbs.

FOOD Gums, flowers and seeds of *Acacia*; fruits and invertebrates.

STATUS Widespread and abundant.

NEEDLE-CLAWED GALAGOS *Euoticus*

Elegant Galago	*Euoticus elegantulus*
Pallid Galago	*Euoticus pallidus*

RECOGNITION Long-limbed, woolly, arboreal galagos with a short, blunt muzzle and very large, pale-orange eyes with rimmed brows. The hands and feet are large in proportion to the body and keels on the fingernails end in a robust, sharp point. They are unique among galagos in having mammae reduced to a single pair. The lower incisors are particularly long and form a sharp blade. Elongated second premolars have bladed tips. They are exceptionally agile runners and can race up or down slanting branches like small monkeys. When they alight on a branch all limbs touch down simultaneously. Their calls are uttered as single, short, disconnected notes with no obvious pattern. Loud calls consist of a short screech, a shrill yap or a loud click. They also make a bird-like 'kweee'.

GENEALOGY Recent genetic studies have confirmed that the closest relative of these highly specialised galagos is the Spectacled Galago, which also has keeled nails and enlarged orbits. Contrary to earlier speculations, *Euoticus* appears to represent the more ancient genus and *Galago* the more derived.

GEOGRAPHY Needle-clawed galagos are restricted to very moist forests between the R. Cross and Congo R., following a distribution pattern that resembles that of many other forest organisms requiring consistently humid conditions. They range up to 1,000m on Mt Cameroun.

ECOLOGY The local abundance of needle-clawed galagos is determined by the distribution of their main food plants: gum-oozing trees and lianas. Up to 80% of their diet may be gums and resins produced by *Newtonia*, rain trees (*Albizia*) and *Albizia/Entada* lianas and this constitutes a year-round staple. Many *Albizia* are fast-growing colonisers and secondary forest plants. They tend to be localised but are often very abundant. They become scarcer in mature primary forest. Needle-claw galagos have been estimated at 3–10 individuals per km^2 in Gabonese primary forest and up to 30 per km^2 in secondary forest. Up to 20% of their food is animal matter (mainly leafhoppers, caterpillars and beetles). The killing and eating of a bird has also been recorded. Fruits are an insignificant part of their diet.

Most frequently seen at between 10 and 25m, needle-clawed galagos nevertheless prefer to travel through the canopy, where they make spectacular leaps in excess of 5m. They can also drop, spread-eagled, from great heights. They are not known to make nests and sleep in huddles of up to five individuals in dense foliage or in the forks of trees. Of all forest prosimians they are the earliest to become active (18.00) and the last to retire (05.45).

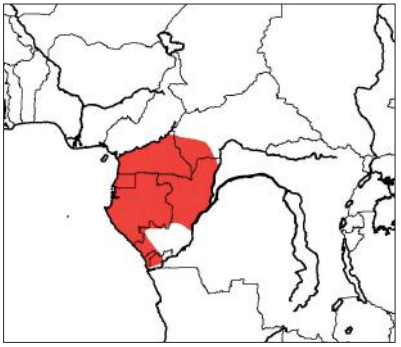
NATURAL HISTORY Groups of females with their offspring can number three or four individuals. They are often joined at their sleeping site by one, sometimes two, adult males. Breeding appears to occur mainly between November and May. Young are 'parked' and the mother's contact call to the young is a short click.

ADAPTATIONS A permanent diet of gums must have been adopted at an early stage in the evolution of these species because their gut shows specialisations not found in other galagos. The delicate incisor and premolar blades are only capable of minor trimming of bark wounds to keep fresh gum flowing and cannot excavate deep initial wounds. In order to harvest sufficient fresh gum, many plant types and a very large number of oozing-sites must be visited each night. The main source of gum droplets comes from bark-wounding by anomalures (see pp.249–50) and fine bore-

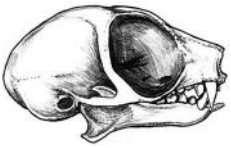
holes drilled by cicadas or the larvae of bark-boring beetles. In central West Africa cicada activity appears to be continuous and on a massive scale, yet needle-clawed galagos hardly ever eat the cicadas themselves. Since several important food trees have a very wide distribution in Africa, the limited distribution of these galagos may be governed by the presence of bark-wounding animals, which make the gum flow in sufficient and reliable quantities for their year-round requirements. Ultimately, large-scale logging is likely to destroy this ecosystem.

The sharp nails from which these galagos get their name, and the exceptionally broad span of their hands and feet, are both adaptations to getting a firm grip on the trunk while feeding. This is particularly important whenever the animals have to bite into or trim the bark but it also allows the galagos to approach gum sites from any position, however awkward.

The structure of needle-clawed galagos' limbs, their habits and their general proportions show an extraordinary degree of convergence with the Malagasy fork-crowned lemur (*Phaner*). The Spectacled Galago (*G. matschiei*), a less consistent gum-feeder, has similar pointed nails.



Elegant Galago



ELEGANT GALAGO *Euoticus elegantulus*

OTHER NAMES Southern Needle-clawed Galago. Fr. *Galago mignon du sud*. Ger. *Sudlicher Kielnagelgalago*.

MEASUREMENTS HB 210mm (180–330mm). T 290mm (280–310mm). W 300g (270–360g).

RECOGNITION Sometimes quite brightly coloured, very agile, long-limbed galago with white underparts sharply divided from foxy-red back by undulating borders. Limbs tawny, face and tail ashy grey or brown. Prominent pale eyes. Voice rather bird-like.

HABITAT Between R. Sanaga and Congo R. in both primary and secondary forests but more common in the latter.

FOOD Gum of rain trees (*Albizia*) and other Mimosaceae and insects. About 5% of the annual diet consists of fruits.

STATUS Widespread and common throughout moist forest belt but likely to be threatened by wholesale logging.

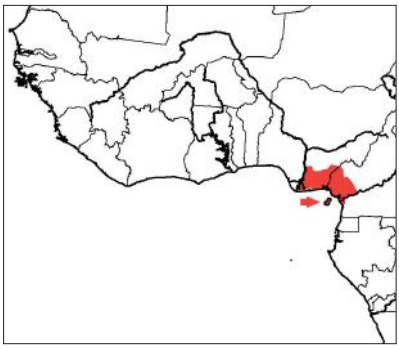
PALLID GALAGO *Euoticus pallidus*

OTHER NAMES Northern Needle-clawed Galago. Fr. *Galago mignon du nord*. Ger. *Nordlicher Kielnagelgalago*.

MEASUREMENTS HB 190mm (170–200mm).
T 280–330mm. W 200–260g.

RECOGNITION A small, very agile dull-coloured galago with yellowish-grey underparts, grey shoulders, arms and tail. The back is brownish with a chocolate-brown dorsal stripe. Both

Pallid Galago



Pallid Galago

needle-clawed species have similar vocal repertoires but the calls of the Pallid Galago may be slightly higher in pitch.

HABITAT Patchily distributed between the Cross R. and R. Sanaga, mainly in secondary forests; also on Bioko I.

FOOD Both needle-clawed species are thought to share a similar dependence on gums and insects.

STATUS IUCN rates as of least concern but intensive logging and fragmentation of the habitat could lead to interruptions in the food chain to which this specialised galago would be vulnerable.

LESSER GALAGOS *Galago*

Spectacled Galago	*Galago matschei*
Senegal Galago	*Galago senegalensis*
Southern Galago	*Galago moholi*
Somali Galago	*Galago gallarum*

RECOGNITION Medium-sized, mostly savanna galagos with grey or brownish backs and round heads with large eyes and short muzzles. Dark eye-masks and pale nose-stripes. Tails not densely furred. All utter short phrases or single cries of regular timing repeated many times. Volume depends on level of excitement of caller. All are agile bounders, landing feet first.

GENEALOGY Recent genetic studies have shown that the more arid-adapted lesser galagos are of relatively late derivation and, unexpectedly, their closest affinities do not lie with the dwarf galagos, which they most superficially resemble. Instead they share ancestry with the forest-dwelling needle-clawed galagos. This confers a new significance on the Spectacled Galago *G. matschei*, as a morphological link between *Galago* and *Euoticus*. Furthermore, this suggests that a reliance on tree exudates (gum), after developing in forest habitats, provided the ancestors of what are now *Acacia*-loving species with a survival strategy in arid habitats.

GEOGRAPHY Split between the northern and southern savannah and the Somali arid zone, the three non-forest species of *Galago* inhabit the entire woodland and treed savanna zones of tropical Africa.

ECOLOGY Woodlands dominated by *Acacia*, *Brachystegia*, *Isoberlinia* and (at much lower densities) mopane (*Colophospermum*) are the preferred habitat of the three non-forest species. The Spectacled Galago inhabits central African forests that share many gummiferous tree genera with these dry woodland types. Gum and insects are the main foods. Other animal foods and fruits are more marginal but can be important locally or seasonally. A single animal may travel 2km in a

night and visit 500 trees but only about 6 hours are actually spent foraging. Where tree hollows are numerous they are used for shelter but tree forks and branch tangles are more generally available. Where neither hollows nor trunks are suitable lesser galagos will make a leaf shelter or take over an old bird's nest as a day-time retreat. Fires represent a major hazard, mainly because they expose lesser galagos to hawks and other predators as they flee.

NATURAL HISTORY Recruitment rates tend to be very high, with females bearing one or two young twice a year. Home ranges of both males and females overlap extensively. Females often share their day-shelter. They are sometimes accompanied by an adult male. Scent-marking with urine, genital rubbing and saliva-dribbling is most intense around sleeping-trees but is maintained at favourite posts scattered around the home-range. The sizes of home-ranges probably vary according to resource availability, habitat type and population density. Gestation periods are in the region of 130 days and the young develop fast, moving out of the nest or hollow at 2 weeks and becoming independent at about 2 months. Females are sexually mature at about 8 months, males at 1 year.

ADAPTATIONS The physiological ability to fuel an energetic lifestyle on gums is the main adaptation that allows these galagos to inhabit dry woodlands and thickets. Their lightning speed during escape and in hunting for prey is another key to their success.

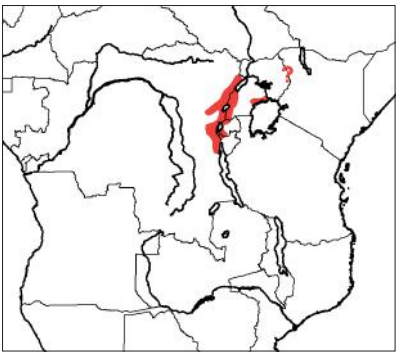
SPECTACLED GALAGO

Galago matschiei (syn. *G. inustus*)

OTHER NAMES Fr. *Galago mignon sombre*. Ger. *Ostlicher Kielnagelgalago*. Swah. *Komba Miwani*.

MEASUREMENTS HB 160mm (147–200mm). T 250mm (190–279mm). W 210g (170–250g).

RECOGNITION A dark-brown, forest-dwelling galago with very large amber eyes surrounded by almost black eye-mask patches. The brown tail is evenly furred along its length. A well-defined ridge borders the eyes, especially at the brows. The lower incisors are sharply protuberant. The nails of hands and feet are keeled and sharply pointed. Yellow secretions are absent in this species.



Spectacled Galago

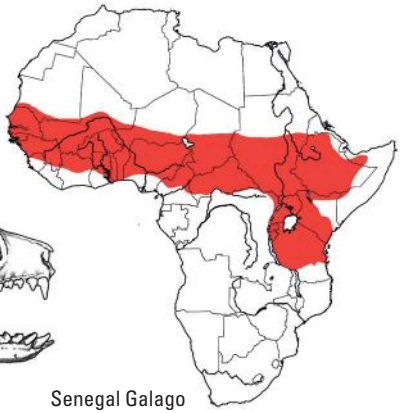
DISTRIBUTION DR Congo east of the R. Lualaba to interlacustrine East Africa, including very isolated mountain slopes in E Uganda.

HABITAT Primary and secondary lowland forest and lower montane forests where *Parinari excelsa* is a dominant tree. The Spectacled Galago can move freely between the canopy and thick tangles at lower levels but is more frequently seen at lower levels.

FOOD Insects, fruits and gums with seasonal changes in preference. Fruits may be a prime choice when available. Caterpillars and beetles are taken during rainy seasons while gums appear to be a dry-season food.

BEHAVIOUR Loud calls are repetitive barks, 'grunt-yaps' and a long, yapping screech. There appears to be a breeding peak in November/December. A pregnant female has also been recorded in February. This species appears to represent an intermediate stage between forest-dwelling *Euoticus* and other gum-eating *Galago* species.

STATUS Widespread but patchy in distribution.



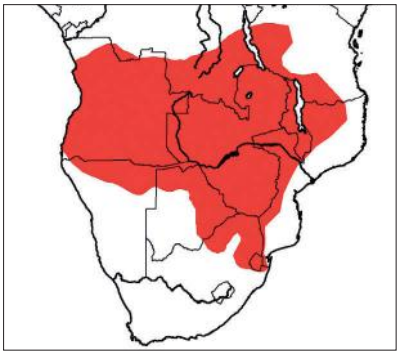
Senegal Galago

SENEGAL GALAGO *Galago senegalensis*

OTHER NAMES Northern Lesser Galago. Fr. *Galago du Sénégal*. Ger. *Senegalgalago*. Swah. *Komba ya Senegal*.
MEASUREMENTS HB 165mm (132–210mm). T 260mm (195–300mm). W 206g (112–300g).
RECOGNITION A long-limbed galago with a long, short-haired tail. The back is grey or brown–grey and the underparts are yellowish (particularly where the two colours meet). Ears are 25–55mm long. The loud advertising call consists of a single, low-pitched note uttered persistently at a regular tempo. (The eye-shine is bright red.)
GEOGRAPHIC VARIATION *G. s. senegalensis* (Senegal to South Sudan and W Uganda), *G. s. braccatus*, also *albipes* and *sotikae* (Uganda, Kenya and N Tanzania), *G. s. dunni* (Ethiopia). The boundaries between these populations are still uncertain.
HABITAT Woodlands dominated by *Acacia*, *Isoberlinia* and *Julbernardia* between Senegal and East Africa; montane forest margins elsewhere. Densely grassed areas are avoided. The exact boundaries of the Senegal Galago's East African range have not been determined.
FOOD Gums, invertebrates and fruits (seasonally). Insects are located and caught with great speed and dexterity on the ground, in flight and on vegetation.
STATUS Widespread and common.

SOUTHERN GALAGO *Galago moholi*

OTHER NAMES Southern Lesser Galago. Fr. *Galago moholi*. Ger. *Moholigalago*. Swah. *Komba ya kusini*.
MEASUREMENTS HB 150mm (88-205mm). T 230mm (110–280mm). W 160g (95–245g).
RECOGNITION Medium-sized to small, greyish or light-brown galago with relatively large ears (20–50mm) and large orange eyes. The eye-mask and tail are dark brownish grey. Legs, feet, forearms and hands have a strong yellowish suffusion. (The eye-shine is red.) The loud advertising call differs from that of the Senegal Galago in being single-, double- and triple-unit cries of high pitch, mixed into series and repeated over long periods.



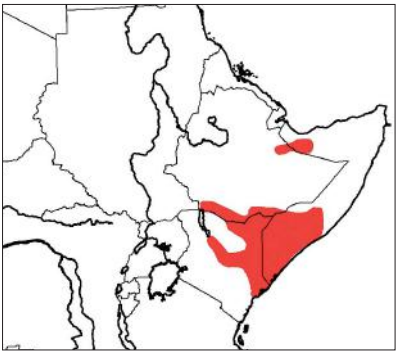
Southern Galago

HABITAT Miombo belt from Angola to W Tanzania, Zimbabwe and the Transvaal. Within this zone the Southern Galago inhabits miombo (*Brachystegia*), *Combretum*, *Acacia* and mopane (*Colophospermum*) woodlands, riverine galleries and forest margins. Its areas of overlap with the

Southern Galago

Senegal, Zanzibar and Mozambique Galagos require further study.
FOOD Acacia and other gums, invertebrates. Fruits are only occasionally taken.
STATUS Common and widespread.

SOMALI GALAGO *Galago gallarum*



Somali Galago

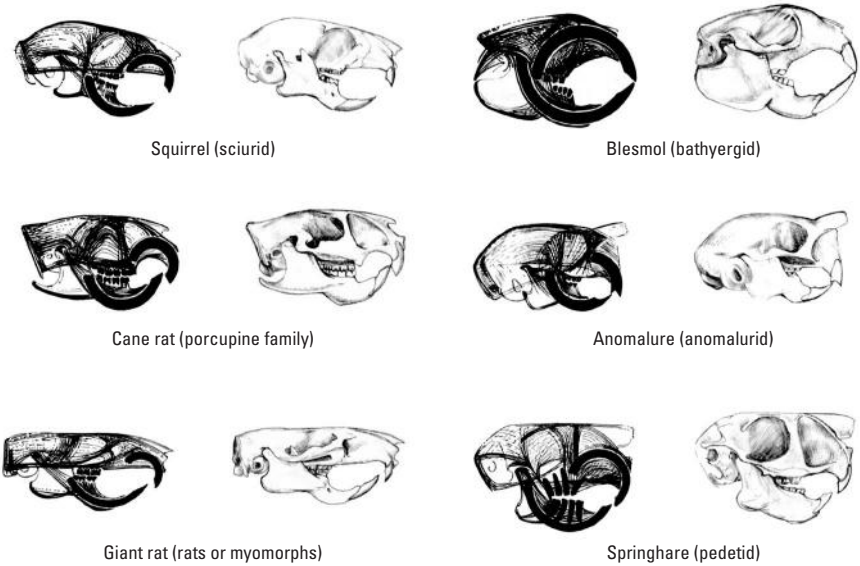
OTHER NAMES Somali Bushbaby. Fr. *Galago de Somalie*. Ger. *Somaligalago*. Swah. *Komba ya Somalia*.
MEASUREMENTS HB 170mm (130–200mm). T 250mm (205–300mm). W 250g.
RECOGNITION Sandy-coloured galago with a broad, round head, medium-sized, black ears (30–40mm), and large eyes only partially surrounded by narrow brown eye-mask. The back is brownish buff and the underparts are off-white with a yellowish boundary between the two colours. The muzzle is black but surrounding facial fur is almost white. Scattered bush may require this galago to spend more time on the ground. Animals have been observed feeding and moving over the ground with long, high bounds. Calls have been described by Dr Thomas Butynski as quacks, yaps, chitters, pings and woos.
HABITAT *Acacia*, *Commiphora* and *Combretum* deciduous bushlands and thickets; known from between the valleys of the R. Wabe Shebelle and R. Tana. The Somali Galago's overlapping boundaries and interactions with the closely related Senegal Galago requires further study.
FOOD Mainly gum and invertebrates with occasional fruits and small vertebrates.
STATUS General degradation of habitats in Somalia may be affecting some populations adversely. Currently unlikely to be endangered overall.

RODENTS RODENTIA

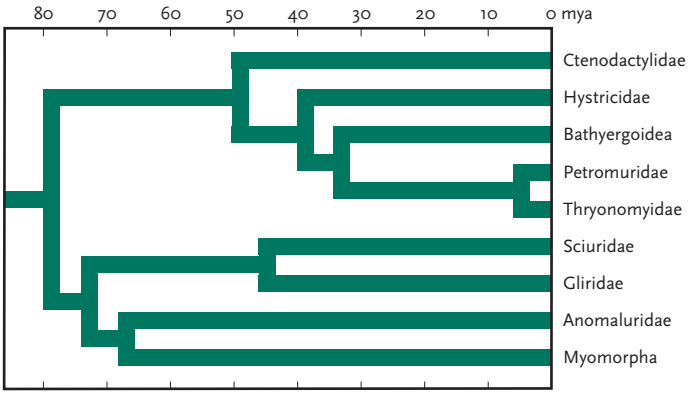
Gundis	Ctenodactylidae
Porcupines	Hystricidae
Cane rats	Thryonomyidae
Noki (Dassie Rat)	Petromuridae
Blesmols	Bathyergidae
Sand-puppy	Heterocephalidae
Squirrels	Sciuridae
Dormice	Myoxidae
Anomalures	Anomaluridae
Springhares	Pedetidae
Jerboas	Dipodidae
Mole-rats and root-rats	Spalacidae
Archaic muroids	Nesomyidae
Cricetid muroids	Cricetidae
Murids	Muridae

Of all the mammalian orders, rodents contain the largest number of species. The most obvious common feature of rodents is their prominent gnawing teeth, two incisors in each jaw with a long space, or diastema, before the cheek-teeth. (As the most diagnostic part of a rodent, frequently found in owl pellets, scats, road-kill and market stalls, skull drawings are included here.) The body build of most rodents is that of conventional quadrupeds but evolution of burrowing, bounding, climbing and gliding has given rise to more specialised body forms in a number of groups.

The four major rodent divisions found in Africa – gundi and porcupine forms (hystricomorphs), squirrel forms (sciuromorphs), anomalures (anomaluromorphs) and rat forms (myomorphs) – have distinctly different arrangements of chewing muscles, orbits and teeth. The gundis, anomalures, springhares and blesmols are all particularly ancient African groups that have become so specialised that their affinities with other rodent groups have only begun to be clarified with the advent of new genetic techniques. Most of these advances in genetics have taken place since the first edition of this guide was published. The new arrangement of taxa broadly follows that of Dr P.-H. Fabre and colleagues.



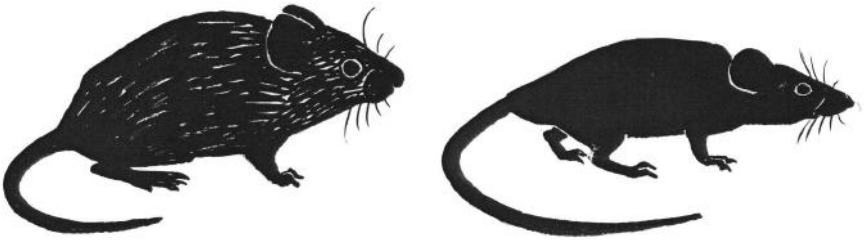
X-rays and skulls showing dentition in six major rodent taxa.



Tentative phylogenetic tree for the Rodentia (mainly after Fabre *et al.* 2012).

Rodent diets are diverse and include animal foods, roots, fruits and seeds. Insectivorous rodents tend to have sharp-cusped molars and a slender muzzle. True herbivores have broad incisors, mill-like grinding teeth and a stout skull, while omnivores tend to be intermediate.

While many rodents have acute sight (especially squirrels) and some are extremely sensitive to sound, all rely heavily on scent (especially in the regulation of their social behaviour). Some rodents are well-known pests and a few can present a threat to human health (notably rats). Periodic population explosions among some species are a particular hazard for rural farmers. Rodents play important structural roles in ecosystems, for example, by pruning or eliminating vegetation types, spreading seeds, creating holes, competing with other animals and facilitating the spread of diseases.



Body form of a herbi-murine (*left*) and omni-murine (*right*).

GUNDIS CTENODACTYLIDAE

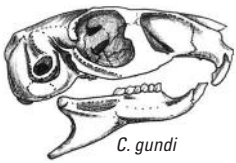
Gundis	*Ctenodactylus* (2 species)
Pectinator	*Pectinator spekei*
Senegal Gundi	*Felovia vae*
Fringe-eared Gundi	*Massouteria mzabi*

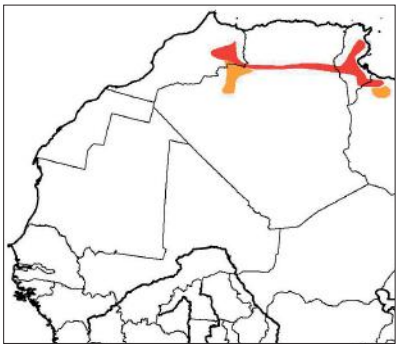
RECOGNITION Compact, brown or tawny animals resembling guinea-pigs, gundis have short legs and blunt, padded toes with tightly curved claws and rows of stiff bristles on the hind feet. The incisor teeth are less hard than in other rodents, so gundis are less consistent gnawers.
GENEALOGY A prediction that gundis represent the stem group for rodents has been borne out by recent genetics. Fossil gundis have been widely recorded from Eurasia where the family is represented at 28 mya. However, gundis derive from early hystricognaths (in turn, possibly derived from zegdoumyids, which have been found at 48-million-year-old sites in Africa).
GEOGRAPHY Now exclusively African, gundis appear to be remnants of a once less specialised rodent group.
ECOLOGY Rock-dwelling, diurnal herbivores in hot deserts, gundis have specialised kidneys that allow them to conserve scarce moisture obtained entirely from the plants they eat. Shortage of water helps explain the curtailed suckling period of gundis and the rapid maturation of the young. Mother gundis wean their two young on chewed plants, and weaning is complete in 4 weeks. This family of rodents does not collect vegetation or make nests.
NATURAL HISTORY Gundis rely on crevices within rock outcrops as refuges but face risks when emerging for food by day. As social animals in dangerous environments they have developed elaborate ways of communicating by voice, scent and tail gestures. They also thump their feet loudly in alarm.
ADAPTATIONS Exposed to extremes of temperature, gundis have developed ultra-fine fur that insulates against both heat and cold. Stiff bristles on the feet serve as a comb for daily grooming sessions. Very sharp, retracted claws allow them to climb steep rocks and trunks.
The food of these animals is scarce and often of poor quality but they are able to conserve energy by adopting a lizard-like strategy of sun-bathing to augment their body temperature in the early morning, followed by retreat into the shade to cool down in the heat of the afternoon. Hearing is extremely well developed. However, this involves enormous internal bullae rather than large external ears.

Gundi is their ancient Berber name.

GUNDIS *Ctenodactylus*

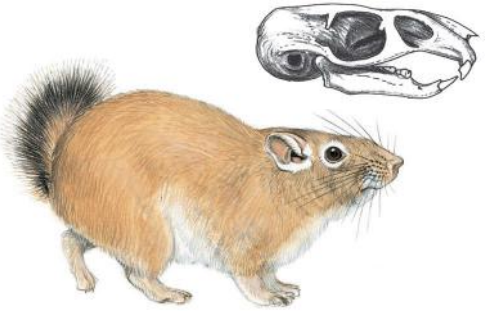
OTHER NAMES Fr. *Goundi*. Ger. *Gundi*.
MEASUREMENTS HB 150–210mm. T 30–50mm. W 175–180g.
RECOGNITION Reddish gundis with a minuscule tail and oval, white-fringed ear. A horny comb is present on the claw of the inner hindtoe. Diurnal, social animals, their whistling or chirping calls can be heard in the early morning.
SPECIES *C. gundi* (near N African coast): chirps. *C. vali* (Sahara desert outcrops): whistles.


C. gundi



Gundis

HABITAT Rock outcrops with abundant crevices in which the gundis shelter singly or in small groups. Two to four young are born during February–April in a secure rocky den. Gundis are extremely agile at running over rocks and when captured will go into spasm.
FOOD Grass, leaves, stalks and flowers, generally grazed or browsed no more than 100m from rocks during morning and evening.
STATUS Not endangered.



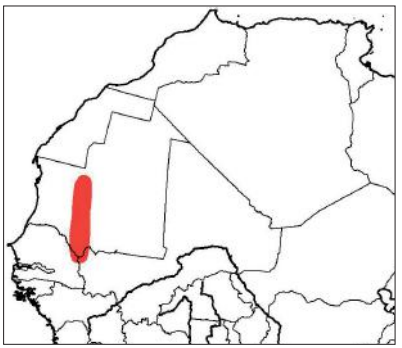
Pectinator

PECTINATOR *Pectinator spekei*

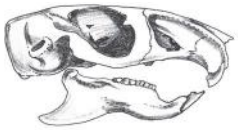
OTHER NAMES Fr. *Pectinator de Speke*. Ger. *Buschschwanz Gundi*.
MEASUREMENTS HB 155–190mm. T 60–80mm. W 168–187g.
RECOGNITION A tawny gundi with a prominent, frequently flicked tail. The muzzle is longer and more pointed than in other gundis and the ears are of a more conventional form. This, the most conservative of gundi species, is more crepuscular than other species, it lives in large, very vocal colonies that emit a variety of chirps and whistles.
HABITAT Rocky outcrops in the Horn of Africa and Ethiopia where home-ranges may be extensive (3km^2).
FOOD A variety of grasses, *Acacia* and other desert plants.
STATUS Scattered occurrence over a large area of distribution. Not endangered.

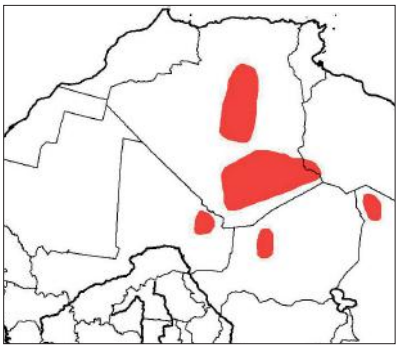
SENEGAL GUNDI *Felovia vae*

OTHER NAMES Fr. *Goundi du Felou*. Ger. *Felou-gundi*.
MEASUREMENTS HB 170–190mm. T 60–80mm. W 177–193g.
RECOGNITION A long-haired, dark walnut-brown gundi with a paler reddish underside and a short but bushy tail. There is an inconspicuous white tuft behind the ears. Incisors are weakly grooved, skull flat and broad. The loud harsh screech of alarm is repeated very persistently.
HABITAT Rock outcrops in dry or semi-arid regions of Mauritania, Mali and Senegal.
FOOD Various grasses, trees and herbs.
STATUS Localised distribution.
IUCN rates as data deficient.



Senegal Gundi





Fringe-eared Gundi

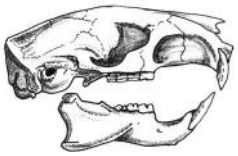
FRINGE-EARED GUNDI *Massouteria mzabi*

OTHER NAMES Fr. *Goundi du Mzab*. Ger. *Sahara-gundi*.
MEASUREMENTS HB 125–210mm. T 30–40mm. W (est.) 132–234g.
RECOGNITION A pale tawny gundi with massively enlarged inner ear bullae opening into a fixed immovable outer ear with complex hair border fringes. The tail is frisked conspicuously. Quieter than other gundis, it only makes occasional chirps.
HABITAT A very low-density species living among rocks in very arid areas of the west and central Sahara Desert and in the Tassili, Hoggar and other massifs. Some regional differences in pelage have been observed.
FOOD Grasses, *Acacia* and other desert plants.
STATUS Very widely, but sparsely and discontinuously distributed. Not endangered.

PORCUPINES HYSTRICIDAE

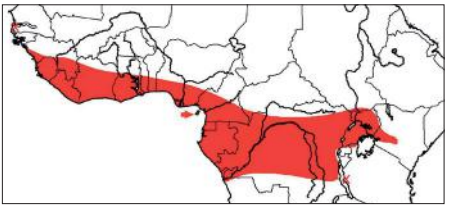
Brush-tailed Porcupine	*Atherurus africanus*
Crested Porcupine	*Hystrix cristata*
South African Porcupine	*Hystrix africaeaustralis*

RECOGNITION Large rodents with spines.
GENEALOGY The most primitive forms (rather like large prickly rats) occur in South-East Asia, where the group probably originated.
GEOGRAPHY Old World from South-East Asia and India to sub-Saharan Africa and parts of the Mediterranean.
ECOLOGY The smaller Brush-tailed Porcupine is exclusively a forest-dweller. The larger species inhabit a wider spectrum of habitats. In their region of overlap (much of Tanzania) the two *Hystrix* species seem to separate by habitat, *H. africaeaustralis* in miombo woodlands, *H. cristata* in drier acacia-woodlands. In captivity the two species fight relentlessly if put together.
NATURAL HISTORY Porcupines are nocturnal herbivores that rely on their spines to deter predators.
ADAPTATIONS The large size and formidable spines of Crested Porcupines can be correlated with movement out of the forest (with relatively few and relatively small predators) into more exposed, non-forest habitats (with many more, large carnivores). At the same time subterranean roots in drier habitats require a good sense of smell and the ability to dig in hard soil; both well-developed faculties in porcupines.



BRUSH-TAILED PORCUPINE

Atherurus africanus



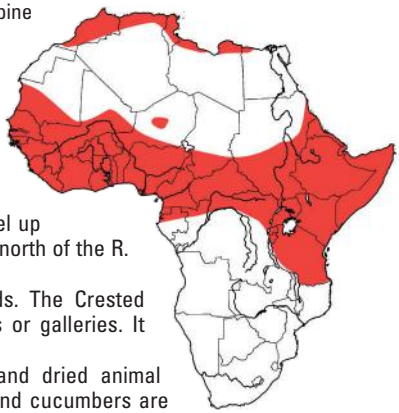
Brush-tailed Porcupine

OTHER NAMES Fr. *Athérure d'Afrique*. Ger. *Quastenstachler*. Swah. *Njiko*.
MEASUREMENTS HB 360–560mm. T 150–230mm. W 2.5–4.0kg.
RECOGNITION A long-bodied, low-slung brown rodent with very bristly fur on the limbs and face, progressing to very sharp, thick quills on the back and shorter ones on the rump and tail. Swollen, hollow white rattle-quills are borne on the tip of the tail. Ears are large and flesh-coloured. The muzzle is swollen. Legs and feet are sturdy.
GEOGRAPHIC VARIATION *A. a. africanus* (West Africa), *A. a. centralis* (Congo basin), *A. a. turneri* (East Africa).
DISTRIBUTION From Sierra Leone to Kenya, from sea level up to 700m within the equatorial zone.
HABITAT Nocturnal inhabitants of rainforests, where a preference for valley bottoms may reflect their need for natural shelters (eroded rock or root systems). Warrens are used for many years and are associated with latrines, habitual radiating trails and, occasionally, 'slides'.
FOOD Fallen fruits, roots, tubers and stems. Oil-palm fruit, crabwood and ginger fruit are especially favoured: animal foods are rarely taken. Brush-tailed Porcupines are masticators rather than gnawers.
BEHAVIOUR Groups of up to 20 animals (usually 6–8) inhabit an area of 2–5ha. They sleep in their burrows during the day and are active much of the night. Brush-tailed Porcupines respond to the attentions of predators by stamping the feet, erecting the spines and thrashing the rattle-tail (the tail easily detaches and is often missing). Captive specimens are very playful.
ADAPTATIONS These porcupines are relatively slow breeders (normally one young but four have been recorded). Young are precocious but do not mature until 2 years old. Up to three litters a year are possible (gestation lasts about 14 weeks). This suggests fairly infrequent predation but the brown (rather than black-and-white) colouring implies a greater vulnerability than that of larger species.
STATUS In the process of being eliminated from many localities due to settlement and over-hunting. Exposure as 'live bushmeat' subjects this species to much cruel ill-treatment. Rated as of least concern.

CRESTED PORCUPINE *Hystrix cristata*

OTHER NAMES Fr. *Porc-épique*. Ger. *Stachelschwein*. Swah. *Nnungu*.
MEASUREMENTS HB 650–1,000mm. T 120–170mm. W 12–27kg.
RECOGNITION A very large, black-bodied, nocturnal rodent with long, black-and-white spines and a prominent crest of elongated, spiny hairs from forehead to shoulders. The Crested Porcupine can be distinguished from the southern species *africaeaustralis* by its black rump and short, rattle-like quills in the tail. The forefeet have strong, digging claws. Fallen quills, tracks and burrows are often the most obvious signs of its presence.

Crested Porcupine



DISTRIBUTION Most non-desert habitats from sea level up to 3,500m, mainly north of the Equator. In East Africa north of the R. Rufiji or R. Ruvuma; also in NW Africa.

HABITAT Savannas, woodlands, steppes and uplands. The Crested Porcupine is sometimes found along forest margins or galleries. It prefers hilly or rocky country.

FOOD Roots, bulbs, bark and fallen fruits. Bones and dried animal remains are frequently gnawed. Root crops, maize and cucumbers are frequently raided.

BEHAVIOUR Family groups often share a burrow or cave but foraging is a solitary activity during which an animal commonly travels up to 15km in a night. Natural holes or crevices are frequently exploited but the Crested Porcupine also digs its own burrow, especially in sandy soils. Galleries are continually expanded so that warrens occupied over many years become very extensive. Up to four young are born within the burrow, possibly twice a year. Baby porcupines are active and mobile at birth. They are suckled for 6 or 7 weeks and travel with the mother for about 1 year.

ADAPTATIONS Hollow rattle-quills in the tail warn off potential predators but their primary role is probably communication with other porcupines, especially during courtship, when both sexes rattle their tails before copulating (carefully).

STATUS Considered an agricultural pest in many areas. Rated as of least concern.

SOUTH AFRICAN PORCUPINE

Hystrix africaeaustralis

OTHER NAMES Fr. *Porc-épic de l'Afrique du Sud*. Ger. *Sud-afrikanisches Stachelschwein*. Swah. *Nnungu*.

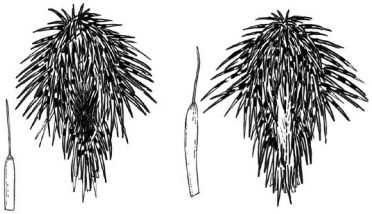
MEASUREMENTS HB 650–1,000mm. T 100–170mm. W 10–24kg.

RECOGNITION A very large, black-and-white rodent with a sweeping, erectile neck crest of white-tipped bristles. Back and tail are covered in black-and-white quills and there is a white rump area. Rattle-quills are 60mm long and conspicuous. The mouth is slightly more overhung by the nose than in the Crested Porcupine. This porcupine usually grunts while foraging.

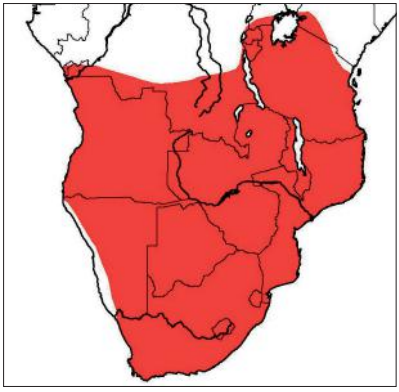
HABITAT Found mainly south of the Equator in most habitats from sea level up to about 3,000m. The South African Porcupine follows routines along regularly used pathways, making detours and pauses to excavate food. It is a summer breeder in South Africa. It matures by 2 years and may live for up to 20 years.

FOOD Mainly roots, bulbs, tubers and bark, with occasional scavenging from carcasses or old skeletons.

STATUS Not endangered (although already eliminated in some settled areas).



Rattle quills and rear views of Crested Porcupine (*left*) and South African Porcupine (*right*).



South African Porcupine

CANE RATS THRYONOMYIDAE

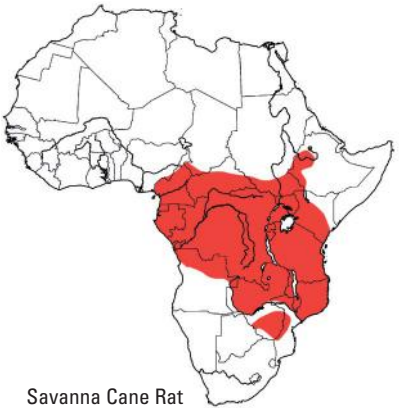
Cane rats *Thryonomys* (2 species)

RECOGNITION Medium-sized to large, robust rodents with grizzled brown coats, prominent chisel-like orange incisors, short tails and short, strong legs with sharp digging claws.
GENEALOGY The cane rat lineage is abundantly represented in the fossil record from about 20 mya; some fossils resemble certain living South American rodents (notably *Carterodon*).
GEOGRAPHY Exclusively African, cane rats have very wide ranges but are absent or rare over much of SW Africa, from the Sahara and from the arid Horn of Africa.
ECOLOGY Dependent on water and coarse valley-bottom grasses, cane rats can be major consumers of mature valley grasses and reeds, for which their cutting teeth and manipulative hands are well adapted.
NATURAL HISTORY Probably territorial, cane rats are highly vocal: they grunt, whistle, hoot and thump their legs (when alarmed on terra firma). Fighting is highly ritualised and serious biting is inhibited. Instead, noses are engaged in weight-testing contests.
ADAPTATIONS At least two litters a year are common, with an average of four young (two to eight) in each litter. Young are born very well developed and are sexually mature and reproductively active by 6 months. Very high levels of reproduction, fuelled by unlimited food, compensates for short life-spans and high mortality rates (cane rats are preferred prey for many carnivores, eagles and humans). The great fecundity of cane rats is effectively exploited by people throughout tropical Africa and some form of 'ranching' might be amenable to systematic management. Confinement in cages has been less successful.

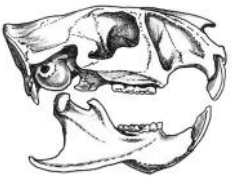
SAVANNA CANE RAT

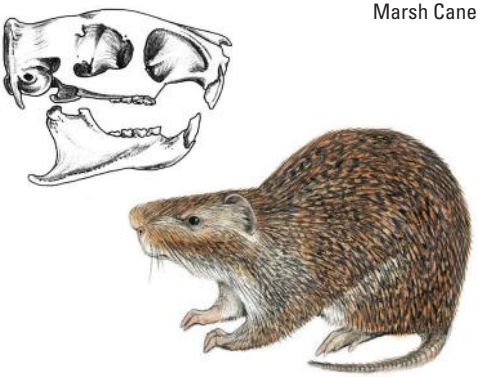
Thryonomys gregorianus

OTHER NAMES Fr. *Petit Aulacode*.
Ger. *Kleine Rohrratte*.
MEASUREMENTS HB 400–560mm. T 110–170mm.
W 2.6–7.5kg.
RECOGNITION A large, grizzled rodent with a bulbous nose, short tail and very deeply grooved incisors. The Savanna Cane Rat is mainly nocturnal and uses habitual paths between feeding areas and shelter. These are often in termitaries or in the holes of other burrowing animals. It sometimes excavates its own shallow holes. Its coarse, stiff hair is frequently to be found in the scats of carnivores.
HABITAT Mainly areas of reliable rainfall and rank grass growth in tropical Africa east of Nigeria. There is much overlap of habitat with the Marsh Cane Rat but the Savanna Cane Rat lives on grassy hills and savannas. It is especially common in Elephant Grass (*Pennisetum purpureum*).

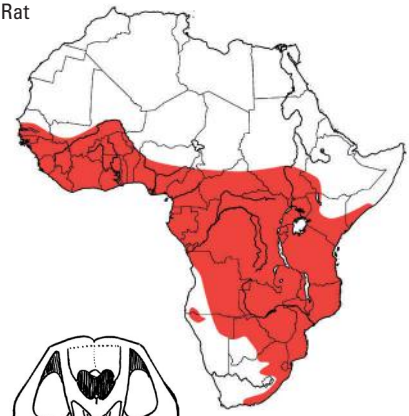

Savanna Cane Rat

FOOD Stems of Elephant Grass; also *Setaria*, *Hyparrhenia*, *Exotheca* and *Melinus*. Ginger (*Aframomum*) is eaten in wet, well-wooded areas. Fruits, bark and roots are also eaten.
STATUS The Savanna Cane Rat has a patchier distribution than the Marsh Cane Rat. Not endangered.





Marsh Cane Rat



incisors

MARSH CANE RAT

Thryonomys swinderianus

OTHER NAMES Fr. *Grand Aulacode*. Ger. *Grosse Rohrratte.*

MEASUREMENTS HB 630–770mm. T 160–195mm. W 3.5–5.2kg.

RECOGNITION Distinguished by its slightly larger size, its longer tail, less protuberant nose and restricted fine grooving of the incisors. The Marsh Cane Rat has a highly characteristic whistle (and foot-thumping in the dry season) and is mainly nocturnal.

HABITAT Beds of *Setaria*, *Echinochloa*, *Sorghastrum* and *Hyparrhenia* in seasonally waterlogged valley bottoms throughout the moister parts of Africa. The pidgin name 'cutting-grass' is an apt description of this cane rat's very rapid and systematic consumption of coarse grass stems.

FOOD Dominant grasses within its habitat.

STATUS Unsuited to small-scale domestication in cages. Well-suited to free-range management. Wide exposure as 'live bushmeat' subjects this species to much cruel ill-treatment.

Marsh Cane Rat, underside showing mouth

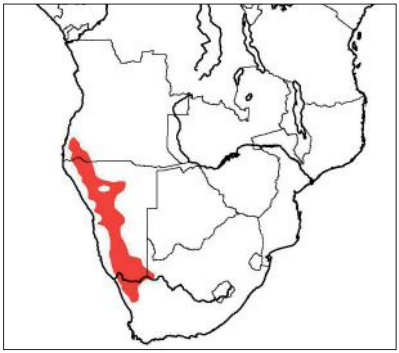
NOKI (DASSIE RAT) PETROMURIDAE

Although the only living representative of this family is the Noki or Dassie Rat *Petromus typicus*, the fossil record reveals petromurids to have been diverse, with two subfamilies and seven genera. Competition from more advanced rodents presumably eliminated them from all but the most specialised of niches in remote localities.

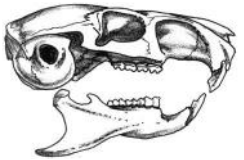
NOKI (DASSIE RAT) *Petromus typicus*

MEASUREMENTS HB 135–224mm. T 115–175mm. W 88–285g.

RECOGNITION A squat, coarse-furred rodent with a long, hairy tail and a peculiarly flattened head. Colour varies from pale grey or ochre, through shades of brown, to nearly black. The feet have rounded, naked pads on the palms and digits (an adaptation for travel on rock). The Noki likes to sunbathe in pairs or small groups but it is very shy and flees for shelter at any disturbance. Urine is used to mark particular rocks and forms characteristic yellow-white streaks near the dens.



Noki



Noki

HABITAT Rocky outcrops in Namibia, N Cape and SW Angola where the Noki shelters in very narrow crevices. Leaf-lined retreats are used as birthing dens for the precocious young.
FOOD Leaves, stems and heads of grasses. The leaves and fruits of shrubs and trees are taken less frequently.
STATUS Rated as of least concern.

BLESMOLS BATHYERGIDAE

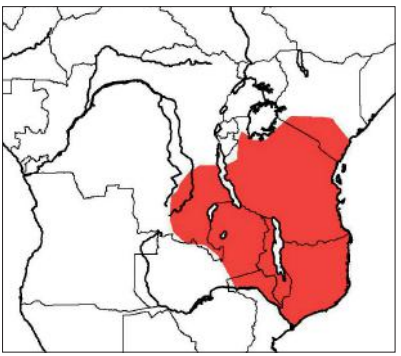
Silky Blesmol	*Heliophobius argenteocinereus*
Dune blesmols	*Bathyergus* (2 species)
Cape Blesmol	*Georychus capensis*
Common blesmols	*Cryptomys* (7 species)

RECOGNITION Compact, subterranean rodents with minuscule eyes and concealed ears. The mouth closes behind the sharp white incisors. Feet are often armed with long claws. The short tail is fringed with hairs in all species. They have great sensitivity to vibrations. Spoil heaps provide the only indication of their presence.
GENEALOGY The anatomy of blesmols is so radically modified and their unique adaptations so ancient that affinities with other rodents were obscure until the advent of molecular genetics.
GEOGRAPHY Exclusively sub-Saharan Africa with the greatest variety in the south. Displaced from NE Africa by Eurasian root-rats (Rhyzomyidae).
ECOLOGY Blesmols dig tunnels with their teeth, assisted by the forepaws, and spoil is pushed out with the rump. The velvety fur is adapted to abrasion and repeated reversals. Their sight is very poor. They display seasonal variations in activity and numbers.
NATURAL HISTORY Most species are solitary or live in small groups but at least one species, the Damaraland Besmol (*Cryptomys damarensis*), is eusocial with 'queen mothers', one reproductive female and a colony of workers.
ADAPTATIONS The prediction that a bee-like social system might be found among mammals living in a closed environment, with a large, storable food supply was confirmed by Dr J. Jarvis's studies of African blesmols.

SILKY BLESMOL (SILVERY MOLE-RAT)

Heliophobius argenteocinereus

MEASUREMENTS HB 100–200mm. T 15–40mm. W 142–168g.
RECOGNITION A long-haired grey blesmol with prominent white incisors. The coat is grey, sandy



Silky Blesmol

or reddish and paler below. White markings on the head or belly are individually variable.

HABITAT Distribution corresponds approximately with the central and eastern areas of miombo (*Brachystegia*) woodlands. Its range overlaps with that of *Cryptomys* but it prefers lower altitudes with a drier climate. It likes well-drained, sandy soils on rocky hillsides, open plains or in woodlands.

FOOD Roots and tubers, including that of a lablab (*Dolichos*) and pulses (*Vigna*).

STATUS Not endangered.

Silky Blesmol

DUNE BLESMOLS (DUNE MOLE-RATS)

Bathyergus

MEASUREMENTS HB 170–330mm. T 30–70mm. W 500–750g.

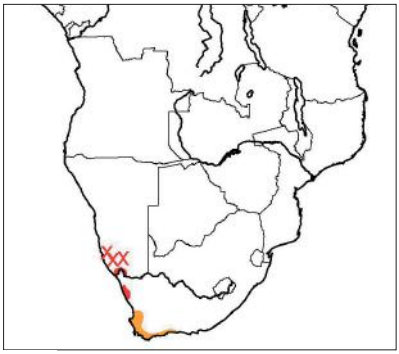
RECOGNITION Large blesmols with long, pointed claws and grooved incisors. Digs with claws, not teeth.

SPECIES Namaqua Dune Blesmol, *B. janetta*: slate-grey and silver. Cape Dune Blesmol, *B. suillus*: large, cinnamon-coloured.

HABITAT Restricted to sandy habitats in extreme south-west of Africa. Dune blesmols live in small groups (of about five) and are very territorial. The most conservative of blesmols.

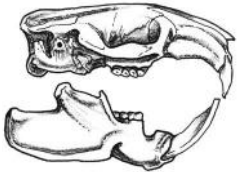
FOOD Roots, bulbs and grass stolons.

STATUS Restricted range in highly populated area. Vulnerable.



Dune blesmols

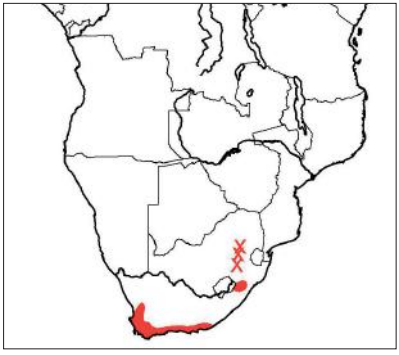
Cape Dune Blesmol
B. suillus



CAPE BLESMOL *Georychus capensis*

MEASUREMENTS HB 140–205mm. T 20–40mm. W 124–360g.

RECOGNITION Surprisingly colourful for a subterranean animal, with a cinnamon and orange back, black head and pale to white underparts. The head resembles a mask, with white surrounding the



Cape Blesmol

vestigial eyes, the ears and also the muzzle, with its prominent teeth. A prolific species, known to have produced as many as 10 young in a single litter.

HABITAT Discontinuous distribution; the Cape littoral and scattered upland areas further to the north-east, coastal sand dunes, and valleys with sandy soils.

FOOD Stores roots and bulbs harvested from very shallow burrows.

STATUS Occurs in several reserves and national parks.

Cape Blesmol

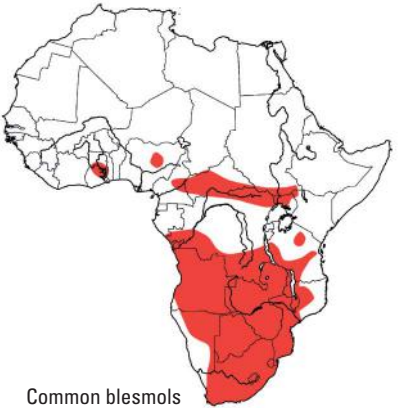
COMMON BLESMOLS *Cryptomys*

OTHER NAMES Mole-rats. Fr. *Rat-taupe.* Ger. *Graumull.*

MEASUREMENTS HB 130–215mm. T 10–25mm. W 100–300g.

RECOGNITION Velvety-furred blesmols with broad palms and relatively small nails (vertically flattened at the front, laterally flattened in the rear, correlating with their respective digging and pushing functions). Eyes and ears are scarcely visible. The white incisor teeth are without grooves.

SPECIES *C. bocagei* (Angola to Zambia), *C. damarensis* (Angola, Namibia to Zambia, Botswana), *C. foxi* (Nigeria), *C. hottentotus* (S Africa to S DR Congo and Tanzania), *C. mechowi* (Angola to Malawi – a large species), *C. ochraceocinereus* (Nigeria to Uganda), *C. zechi* (Ghana, Togo). (Note that much confusion persists over names and distributions.)

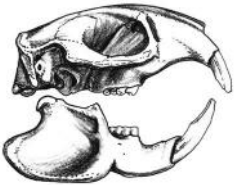


Common blesmols

HABITAT Drier soils outside main forest blocks.

FOOD Roots, bulbs, grass, leaves and occasional invertebrates.

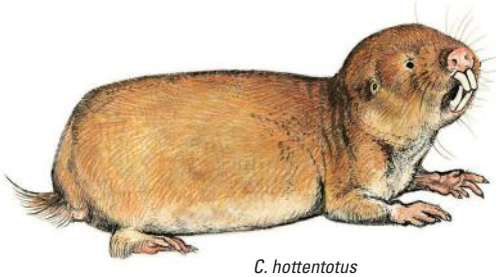
BEHAVIOUR Food-gathering is seasonal; burrows are extended in the rains and collected roots brought back to stores. Colonies vary in size and some species are solitary. *C. damarensis* colonies average 16 animals with only one reproductive male and female. The rest of the colony collect roots in a central store, dig new galleries and feed, groom and warm the 1–6 young that are born to the 'queen' two or three times a year. If the queen dies, subordinate females fail to take her place, as happens with Sand-puppies (Naked Mole-rats).



C. mechowi

ADAPTATIONS The adaptations of these blesmols are sufficiently similar to those of the root-rat (*Tachyoryctes*) for the two to be mutually exclusive. The blesmols' overall range is interrupted in NE Africa where they have presumably been replaced.

STATUS Some species (notably *C. mechowi* and *C. foxi*) may be endangered by the spread of agriculture.



C. hottentotus

SAND-PUPPY HETEROCEPHALIDAE

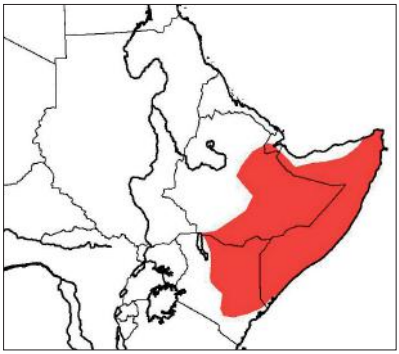
First proposed in 1957, this family is now confirmed as a genetically distinct and ancient family. The single species is closely related to the blesmols (see p.221) and is eusocial, a feature it shares with at least one blesmol. Unlike the blesmols, the Sand-puppy is hairless.

SAND-PUPPY (NAKED MOLE-RAT)

Heterocephalus glaber

MEASUREMENTS HB 80–100mm. T 20–50mm. W 30–80g.

RECOGNITION A small, naked rodent resembling a newborn, even foetal, animal. Its transparent skin goes pale parchment or bright red depending on body heat and circulation. Within a colony of about 75 animals different castes can be distinguished by size and by their role in the 'hive'. Largest is the breeding female, attended by 'drones' or non-working adults, of medium size. 'Workers' (communal diggers, foragers and carriers) are the smallest animals. The usual sign of the Sand-puppy's presence is little volcano-shaped spoil heaps.



Sand-puppy

DISTRIBUTION Confined to Horn of Africa, living in a variety of mostly hard, compacted soils in a hot, dry climate. Fossils found further south in Tanzania suggest a wider range during past, drier periods.

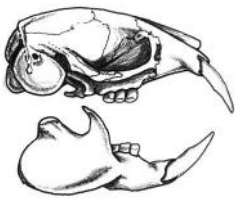
HABITAT Plains, thickets, dry savannas and open woodlands, i.e. areas with abundant plants bearing subterranean storage organs and edible roots. The micro-climate within Sand-puppy burrows is very stable (about 30° C).

FOOD The roots of dominant trees, such as *Acacia* and *Commiphora*, the vine *Cissus*, lilies (*Ammocharis*) and the bulbs and tubers of other common plants. Such roots are eaten in situ and the plant is often not killed because only the 'store' is taken.

BEHAVIOUR The Sand-puppy is celebrated as the prime example of a highly social mammal which exhibits division of labour (as in bees and termites). As with bees, the life of the colony is governed through chemical mechanisms. The dominant female generates stress and produces scents (pheromones) that suppress sexual development and growth in all other females. All the colony share a single nest and are communally affected by the 'queen's' current sexual condition (for example both sexes develop teats just before she gives birth). Her young become workers on weaning.

ADAPTATIONS The eusocial lifestyle appears to have evolved in order to cope with the difficulties that a single pair of animals would face gathering food, breeding, raising offspring and keeping secure from predators in the habitat occupied by the Sand-puppy. The benefits of safety from predation, secured by a wholly subterranean existence, is compromised by the hardness of the ground. Soil hardness also makes foraging for scattered and patchy foods a huge labour. By specialising in digging and foraging, workers are able to supply adequate food for a colony of closely related brothers and sisters while the 'queen' ensures continuity by producing up to four litters a year each numbering about 12 babies (as many as 27 have been recorded in captive animals).

STATUS Very widespread.



SQUIRRELS SCIURIDAE

Sun squirrels	*Heliosciurus* (6 species)
African Pygmy Squirrel	*Myosciurus pumilio*
African Giant Squirrel	*Protoxerus stangeri*
Slender-tailed Squirrel	*Allosciurus aubinnii*
Palm squirrels	*Epixerus* (2 species)
Rope squirrels	*Funisciurus* (10 species)
Bush squirrels	*Paraxerus* (10 species)
Ground squirrels	*Xerus* (5 species)

The name 'squirrel' is an anglicisation of the Greek *skiouros*, meaning 'shade-tail', a well-observed, hot-weather use for these animals' conspicuous, furry tail, but it primarily serves as a scent-dispenser and communication device or flag. Some squirrels are brightly coloured, with red tints or body stripes, indicating that vision is an important sense. The eyes are relatively large, ears small and the head tends to be blunt and round, with powerful muscles for gnawing hard foods. Most are competent climbers.

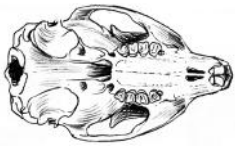
It is thought that two separate ancestral squirrels arrived from Eurasia during the mid-Miocene, possibly in the form of two single species. The earlier immigrant gave rise to all the arboreal species, radiating into four or five main groups. Sun squirrels (*Heliosciurus*), are arboreal, forest and woodland squirrels, strongly diurnal (hence their name). The African Pygmy Squirrel (*Myosciurus pumilio*) is a miniature specialist restricted to leguminous forests in the 'arm-pit of Africa' and at the other end of the size scale, the African Giant Squirrel *Protoxerus stangeri* (and allies *Epixerus* and *Allosciurus*) are large nut-eating specialists. The more omnivorous and medium-to-small rope squirrels (*Funisciurus*) have a mainly centre–west, equatorial distribution, while the closely related bush squirrels (*Paraxerus*) radiated in the south-east realm with a few species adapting to the eastern Congo forests.

The second, later, immigrant was a mainly terrestrial squirrel whose descendants are the ground squirrels (now all classed as *Xerus*).

Most squirrels build nests but many use tree or ground holes. Many species are highly vocal and sound, scent and sight are all employed in their signalling behaviour. Squirrels tend to be conspicuous and all known species are profiled here because, like monkeys, they readily catch the attention of naturalists and can be identified by external clues alone.

SUN SQUIRRELS *Heliosciurus*

Rwenzori Sun Squirrel	*Heliosciurus ruwenzori*
Zanj Sun Squirrel	*Heliosciurus undulatus*
Mutable Sun Squirrel	*Heliosciurus mutabilis*
Red-legged Sun Squirrel	*Heliosciurus rufobrachium*
Gambian Sun Squirrel	*Heliosciurus gambianus*
Punctate Sun Squirrel	*Heliosciurus punctatus*



H. ruwenzori

An exclusively African group of diurnal squirrels that are entirely tropical, although some species inhabit equatorial highlands.

RWENZORI SUN SQUIRREL

Heliosciurus ruwenzori

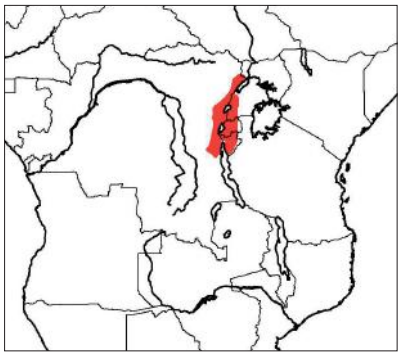
OTHER NAMES Fr. *Héliosciure du Ruwenzori*. Ger. *Ruwenzori Sonnenhörnchen*.
MEASUREMENTS HB 200–260mm. T 220–280mm. W 205–377g.
RECOGNITION Thickly and densely furred squirrel with a grizzled grey upperside contrasting strongly

with the white underside. The tail is boldly barred in grey and white. Vestigial teeth suggest that this species, in common with some other genera, may retain some characteristics of the earliest ancestral squirrels. The Rwenzori Sun Squirrel tends to carry the tail in line with the body.

HABITAT Montane forests between 1,600 and 2,700m in E DR Congo and W Uganda, Rwanda and Burundi. This species has adapted to secondary growth and cultivation mosaics.

FOOD Fruits of dominant trees. Insects and lichen have also been recorded.

STATUS In spite of its limited range, IUCN rates this species as of least concern.



Rwenzori Sun Squirrel

ZANJ SUN SQUIRREL

Heliosciurus undulatus

OTHER NAMES Fr. *Hélioscuire de Zanj*.
Ger. *Zanj Sonnenhörnchen*.

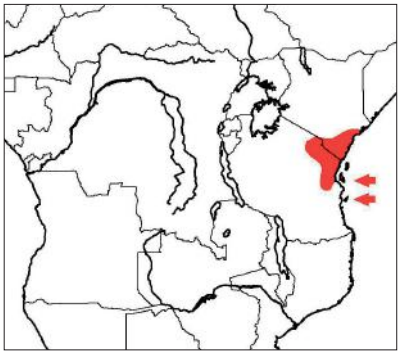
MEASUREMENTS HB 200–250mm. T 210–280mm. W (est.) 250–380g.

RECOGNITION The back is tawny grizzled and underparts are cream. The tail is barred in brown and cream.

HABITAT Lowland and montane forests and thickets, and secondary growth, east of the Gregory Rift from Mt Kenya to R. Rufiji, and on Zanzibar and Mafia Is. Nests in hollow trees or branches.

FOOD Fruits and seeds, palm dates, leaves and buds. Insects are of seasonal importance.

STATUS IUCN categorises as data deficient.



Zanj Sun Squirrel

Zanj Sun Squirrel

Mutable Sun Squirrel

MUTABLE SUN SQUIRREL

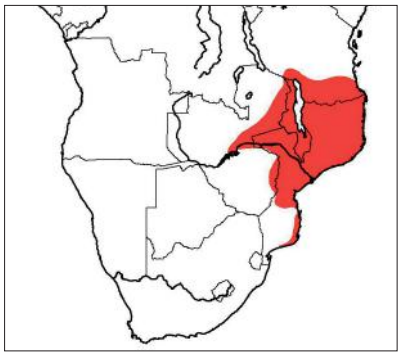
Heliosciurus mutabilis

OTHER NAMES Fr. *Hélioscuire variable*.
Ger. *Mutables Sonnenhörnchen*.

MEASUREMENTS HB 210–280mm. T 210–300mm. W 200–380g.

RECOGNITION Upperparts are grizzled brown or orange, with tones from pale to nearly black. Underparts also vary from white to fawn or grey. The tail has a narrow, indistinct barring in similar tints to the body.

HABITAT Lowland to montane forests and thickets,

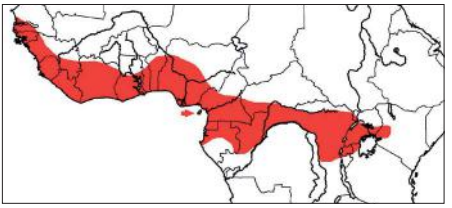


Mutable Sun Squirrel

including riverine strips and cultivation mosaics, from the R. Rufiji southwards to Zimbabwe and Mozambique.
FOOD Various plant foods; occasionally insects and small vertebrates.
STATUS Common.

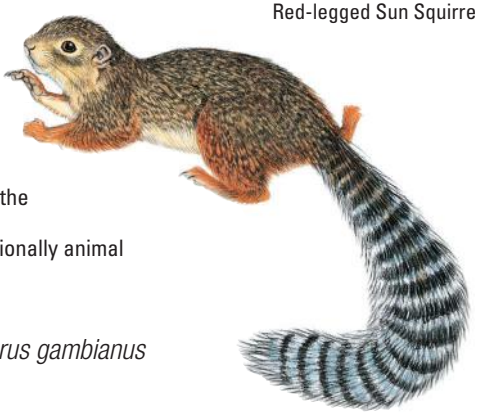
RED-LEGGED SUN SQUIRREL

Heliosciurus rufobrachium



Red-legged Sun Squirrel

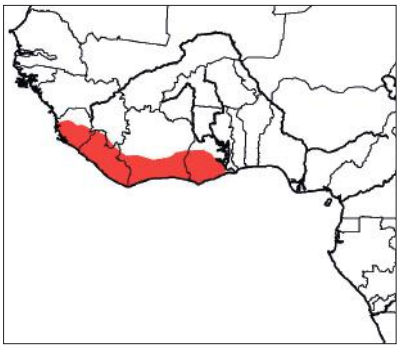
OTHER NAMES Fr. *Héliosciure à pattes rousses*. Ger. *Rotbein Sonnenhörnchen*.
MEASUREMENTS HB 200–250mm. T 210–270mm. W 290–420g.
RECOGNITION Upperparts are grizzled, graduating to warm reddish tints on the outer surfaces of the limbs. The underside is paler cream-coloured (often with sparse fur). The long tail is barred with black and white (about 18 bands of each). Loud calls and a flicking tail are particularly noticeable.
HABITAT Very common at low and medium altitudes from Senegal eastwards across the Congo basin to Uganda to the Gregory Rift.
FOOD Fruits, palm dates, leaves, buds; occasionally animal material.
STATUS Widespread and common.



GAMBIAN SUN SQUIRREL *Heliosciurus gambianus*

OTHER NAMES Fr. *Héliosciure de Gambie*. Ger. *Gambisches Sonnenhörnchen*.
MEASUREMENTS HB 170–240mm. T 180–260mm. W 250–350g.
RECOGNITION Variably coloured squirrel with a grizzled back and head and lighter underparts. The tail is boldly barred (about 14 rings) and there is a pale surround to the eyes.
HABITAT Woodlands and savannas and montane habitats from Senegal to Ethiopia and Kenya; south of the forest block from Angola to Tanzania. Enclaves in forest areas are considered to be the product of 'engulfment' after changes in climate. It descends to the ground to visit isolated trees but prefers branch travel.
FOOD Fruits, seeds and the pods of *Acacia*; animal foods are also taken.
STATUS Widespread and common.

Gambian Sun Squirrel



Punctate Sun Squirrel

PUNCTATE SUN SQUIRREL

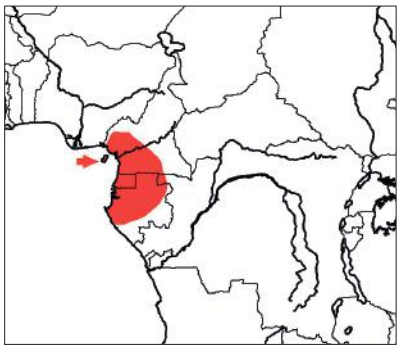
Heliosciurus punctatus

OTHER NAMES Small Sun Squirrel. Fr. *Helioscuire de foret.* Ger *Gerflecktes sonnenhörnchen.*
MEASUREMENTS HB 223–294mm. T 112–230mm. W109–256g.
RECOGNITION A dark, grizzled forest squirrel with a slender, ringed tail.
HABITAT Secondary and primary rainforest in Upper Guinea.
FOOD Seeds and fruits.
STATUS Little known and IUCN categorises as data deficient.

AFRICAN PYGMY SQUIRREL

Myosciurus pumilio

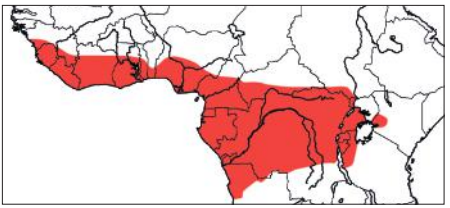
OTHER NAMES Fr. *Ecureuil pygmée.*
Ger. *Afrikanischer Zwerghörnchen.*
MEASUREMENTS HB 61–74mm. T 45–60mm.
W 12.4–20.0g.
RECOGNITION Extremely small, mahogany-coloured squirrel with pale underparts, cream-coloured fur around the eye and mouth, and white ears. The tail has a reddish base and a darker terminal bush. A shy species, tending to hide at any disturbance, but it can move very fast.
HABITAT Only found in the wettest area of the Bight of Biafra, from the Cross R. to S Gabon. It lives on the trunks and larger branches of large trees in primary forest and shows a strong preference for caesalpinoid-dominated tree communities, where bark exudates, possibly including fungi and lichens, as well as fruits and insects, are thought to be the main food source. It is not known to cache food.
FOOD Forages, with a splayed, lizard-like gait, for bark scrapings, invertebrates (often from resin sites where gums are ignored) also buds, young leaves and fruits.
STATUS Although locally abundant, this squirrel is probably declining due to felling of primary forests. Previously classed as vulnerable, IUCN now rates it as of least concern.



African Pygmy Squirrel

AFRICAN GIANT SQUIRREL

Protoxerus stangeri



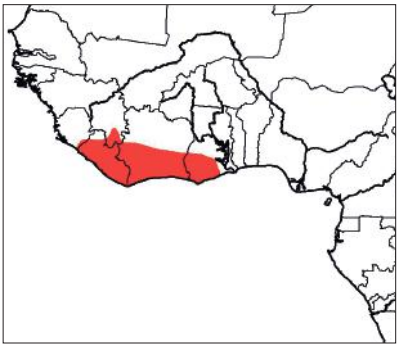
African Giant Squirrel

OTHER NAMES Forest Giant Squirrel. Fr. *Grand écureuil de Stanger*. Ger. *Olpalmenhörnchen*.
MEASUREMENTS HB 220–400mm. T 240–360mm. W 530–800g.
RECOGNITION Large, grizzled squirrel with a disproportionately large, rounded head which is predominantly grey. The back and limbs are of warm tints, very variable in colour and intensity. The yellowish underside is often semi-naked. Nose, ears and eyelids also tend to be naked. The long, black-and-white tail has about 18 bars. Nineteen subspecies have been described including *P. s. cooperi* in NW Tanzania.

HABITAT Well-developed equatorial rainforests, in tall swamp forest and at altitudes up to 2,000m.
FOOD Mainly fruits, seeds and nut kernels of numerous rainforest trees (87.6% in Gabon, with 8.5% leaves, 3.5% mushrooms and traces of animal matter).
STATUS IUCN rates as of least concern.

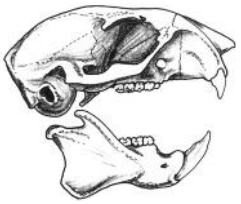
SLENDER-TAILED SQUIRREL

Allosciurus aubinnii



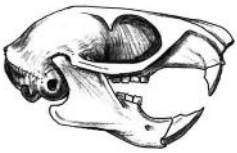
Slender-tailed Squirrel

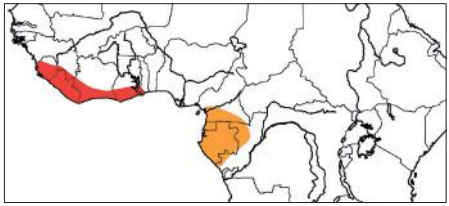
OTHER NAMES Aubinn's Squirrel. Fr. *Ecureuil d'Aubinn*. Ger. *Dunnschwanzhörnchen*.
MEASUREMENTS HB 230–270mm. T 270–330mm. W (est.) 300–400g.
RECOGNITION A largish, very dark squirrel with a long, slender, tapered tail with very fine black-and-olive annulations. The short, dense coat is very fine and silky and covers upper and underparts equally.
HABITAT Moist high forests from Liberia to Ghana, with a marked preference for palms.
FOOD Fruits, particularly palm dates. Unlike the African Giant Squirrel, which prefers to eat only the kernels, this species has been recorded feeding on the husks.
STATUS Rare. Probably endangered over most of its range; IUCN lists as data deficient.



PALM SQUIRRELS *Epixerus*

Western Palm Squirrel	*Epixerus ebii*
Biafran Bight Palm Squirrel	*Epixerus wilsoni*





Western Palm Squirrel
Biafran Bight Palm Squirrel

WESTERN PALM SQUIRREL

Epixerus ebii

OTHER NAMES Fr. *Ecureuil d'Ebi*.
Ger. *Nachtbauchhörnchen*.
MEASUREMENTS HB 260–310mm. T 250–310mm. W 540–650g.
RECOGNITION Large squirrel with a grizzled grey back and a warm orange-to-red underside. The very conspicuous black-fringed tail has black-and-white bars across the upperside and fine longitudinal stripes, fading into an orange brush, on the underside. The muzzle is more protuberant than in the African Giant Squirrel.
HABITAT Palm forests and mature rainforest in mainly coastal areas from Sierra Leone to Ghana.
FOOD Fruits and nuts are collected on the tree or from the ground.
STATUS Range greatly contracted due to logging of primary rainforests. Rare, with large ranges; intolerant of secondary growth.

BIAFRAN BIGHT PALM SQUIRREL

Epixerus wilsoni

OTHER NAMES Fr. *Ecureuil du Biafra*.
Ger. *Biafra Bauchhörnchen*.
MEASUREMENTS HB (est.) 260–290mm. T 270–310mm. W 500–620g.
RECOGNITION Large squirrel with a grizzled grey back. The face and underparts are cream, with warmer tints on the wrists and rump. The tail has a predominantly white upperside, with bold black bars or chevrons and a warm-coloured stem on the underside. The head is broad and flat, with a long robust muzzle. (It is distinguishable from the western species mainly by cranial differences.)
HABITAT Lowland rainforests near the coast from S Cameroon to Congo R. Areas with abundant palms are preferred.
FOOD Fruits and nuts (98% in Gabon); occasionally animal foods.
STATUS Rare.

ROPE SQUIRRELS *Funisciurus*

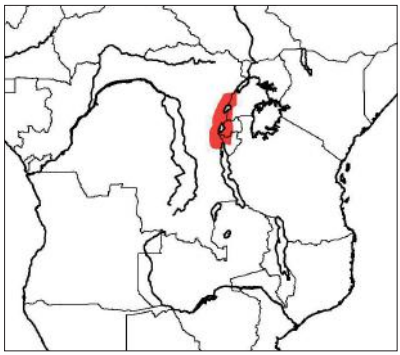
Carruthers's Mountain Squirrel	*Funisciurus carruthersi*
Ribboned Rope Squirrel	*Funisciurus lemniscatus*
Lunda Rope Squirrel	*Funisciurus bayoni*
Thomas's Rope Squirrel	*Funisciurus anerythrus*
Red-cheeked Rope Squirrel	*Funisciurus leucogenys*
Fire-footed Rope Squirrel	*Funisciurus pyrropus*
Kintampo Rope Squirrel	*Funisciurus substriatus*
Du Chaillu's Rope Squirrel	*Funisciurus duchaillui*
Lady Burton's Rope Squirrel	*Funisciurus isabella*
Congo Rope Squirrel	*Funisciurus congicus*

RECOGNITION Small, thin, soft-furred squirrels with a fluffy, rather flimsy tail that is frequently carried curled over the back and is continuously flicked. Tail jerks are sometimes synchronised with loud territorial or warning calls. Some species have red or yellowish tints, pale side-stripes or even spots. In spite of loud calls and a tendency to approach disturbances, the dark colours of rope squirrels are difficult to see and their main defence is to freeze or move behind the nearest tree.
GENEALOGY Rope squirrels have differentiated in diet and in their degree of arborealism. Carruthers's Mountain Squirrel links *Funisciurus* with *Paraxerus* and is probably the most conservative species. The most terrestrial and insectivorous is the Ribboned Rope Squirrel, *F. lemniscatus* (the little-known Lunda Rope Squirrel, *F. bayoni*, may be its counterpart south of the Congo R.). By contrast, Lady Burton's (*F. isabella*), Kintampo (*F. substriatus*) and Congo (*F. congicus*) Rope Squirrels are predominantly fruit- and leaf-eaters that spend more time in the trees. Successful species with a wide range (and somewhat intermediate between the two previous groups) are the Fire-footed (*F. pyrropus*), Red-cheeked (*F. leucogenys*) and Thomas's (*F. anerythrus*) Rope Squirrels. Primary divergences in diet may have been followed by separation in response to past changes in climate and as a result of isolation of populations. During wet phases Fire-foots, true forest species, would have been dominant. During drier, glacial periods the more strictly riverine Thomas's might have been favoured. Today their ranges interdigitate or overlap.
GEOGRAPHY Rope squirrels tend to live in dark, shady habitats but, in common with all squirrels, like to sunbathe in transitory shafts of light. Their almost exclusive equatorial and mainly lowland West African distribution may reflect a compromise between sensitivity to cold and adaptation to life on the forest floor.
ECOLOGY Ground-dwelling is combined with a tendency to hoard (they may be important dispersers and planters for some tree species). The divergence between more and less insectivorous species reflects the need for different physiologies and strategies in exploiting the rich resources of fallen fruits and insects on the forest floor. Rope squirrels tend to use habitual feeding stations (generally a raised root with a good view of the surroundings). They are frequent prey to forest birds of prey and, possibly, to snakes.
NATURAL HISTORY Frequent noisy contacts between rope squirrels constitutes an aspect of their territorial behaviour, as does their use of scent, which is strong even to the human nose. Rope squirrels mob snakes, birds and large mammals with bird-like chirps which are extremely difficult to locate and are combined with rapid advances and retreats. Oestrous females advertise their condition with sound and scent.
ADAPTATIONS Complex nest-making behaviour, which includes laborious daily shredding of bark, palm leaves or other fibres, appears to be necessary to maintain warm, dry nesting conditions. Their large nests are concealed (usually at low levels) in buttresses, palm-frond bases or in hollow or perforated trunks. Such behaviour may have facilitated their colonisation of a dark, wet habitat.

CARRUTHERS'S MOUNTAIN SQUIRREL *Funisciurus carruthersi*

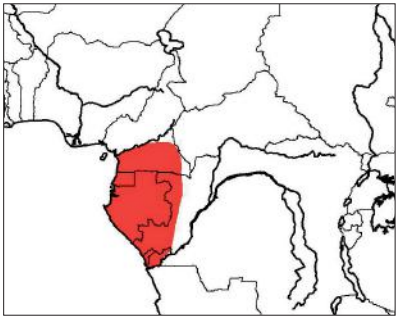
OTHER NAMES Carruthers's Rope Squirrel. Fr. *Funisciure de montagne*. Ger. *Bergstreifenhörnchen*.
MEASUREMENTS HB 200–260mm. T 180–200mm. W 200–336g.
RECOGNITION Olive-green squirrel with a cloud-grey underside and a black-and-yellow barred tail with a black tip. Rings of pale cream-coloured fur surround the eyes.

Carruther's Mountain Squirrel



Carruther's Mountain Squirrel

HABITAT Between 1,500 and 2,800m in the mountain chains of E DR Congo and W Uganda, especially in stands of African wild plums (*Prunus africanum*), a dominant tree of the area. Large, globular nests, lined with finely shredded bark, are constructed in dense tangles. This squirrel ranges through all vegetation levels and frequently spends time on the ground.
FOOD Various fruits and seeds (e.g. *Bridelia* and *Strombosia*); occasionally insects.
STATUS Common within several national parks. Of special interest as a morphological 'bridge' combining characteristics of *Funisciurus* and *Paraxerus*. Not endangered.



Ribboned Rope Squirrel

RIBBONED ROPE SQUIRREL *Funisciurus lemniscatus*

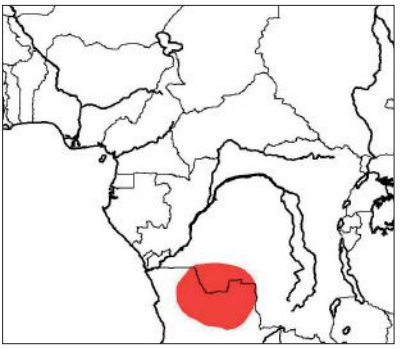
OTHER NAMES Fr. *Funisciure rayé*. Ger. *Streifiges Baumhörnchen*.
MEASUREMENTS HB 150–180mm. T 130–190mm. W 100–150g.
RECOGNITION A small, olive-coloured squirrel with two dark and two pale stripes restricted to the flanks.
HABITAT Ranges from R. Sanaga to Congo R. and R. Aruwimi; predominantly terrestrial.
FOOD About 40% animal matter and 60% fruits and seeds. Leaves and mushrooms are occasionally taken. Almost all food is collected on the ground.
STATUS Not endangered.

LUNDA ROPE SQUIRREL

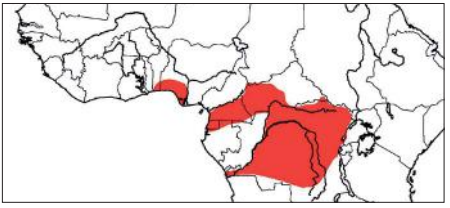
Funisciurus bayonii

OTHER NAMES Fr. *Funisciure de Bocage*.
Ger. *Bocages Streifenhörnchen*.
MEASUREMENTS HB 160–195mm. T 130–170mm.
W 110–160g.
RECOGNITION The back is greyish olive-green, with a fine black grizzle and the underside is pale grey. There is a pale eye-

ring and a poorly defined pale stripe on flanks. The indistinctly barred tail has hairs broadly banded in black and white near their tips.
HABITAT Mosaic of rainforest and moist woodlands in NE Angola and SW DR Congo.
FOOD Not known (if research in this area is carried out it may provide clues to this species' affinity with other rope squirrels).
STATUS Insufficiently known.



Lunda Rope Squirrel



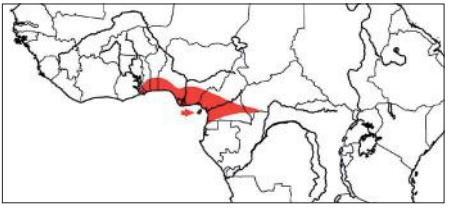
Thomas's Rope Squirrel

THOMAS'S ROPE SQUIRREL *Funisciurus anerythrus*

OTHER NAMES Redless Tree Squirrel. Fr. *Funisciure de Thomas*. Ger. *Rotloses Baumhörnchen*.
MEASUREMENTS HB 160–230mm. T 130–200mm. W 200–220g.
RECOGNITION The back is brownish olive, with variable pale flank stripes. The underside is grey or buff. The tail has a light 'halo' over a broad band of very dark grey. The base of the tail hairs is greyish or dull orange.
HABITAT Predominantly recorded from the margins of the Congo R., R. Ogooué and other rivers from Nigeria to Uganda in the north, and from Angola to S DR Congo. Lives in the lower strata of dense secondary growth along the margins of rivers and swamps, spending much of its time on the ground.
FOOD In Gabon, about 80% fruits and 20% animal matter. Leaves and mushrooms are occasionally taken.
STATUS Widespread and common. Considered a pest of cocoa in some areas.

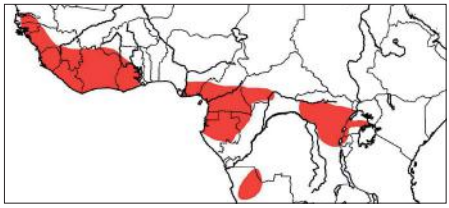
RED-CHEEKED ROPE SQUIRREL
Funisciurus leucogenys

OTHER NAMES Fr. *Funisciure à tête orange*.
Ger. *Orangenkopfiges Baumhörnchen*.
MEASUREMENTS HB 170–215mm. T 130–200mm. W 200–300g.
RECOGNITION A small squirrel of rather variable tints. The olive-brown back is punctuated by a line of pale or orange

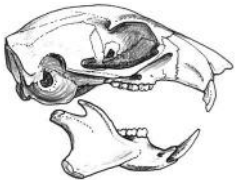


Red-cheeked Rope Squirrel

dashes or spots running over the flank from shoulder to haunch. The face is usually orange-red. The underside is grey or pale orange. The bases of the tail hair show as a broad orange midline from below but terminal black and white bands make a bold cross-bar pattern from above.
HABITAT Lowland and montane forests from the R. Volta eastwards to the R. Ubangi and Congo R.; also Bioko I. Restricted to forest floor and low levels in old mature rainforest.
FOOD Not known in detail. Mainly fallen fruits.
STATUS A wide range suggests that this species is not endangered overall , but declining locally with felling of primary forest.



Fire-footed Rope Squirrel



FIRE-FOOTED ROPE SQUIRREL

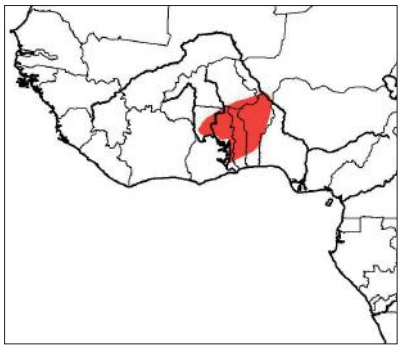
Funisciurus pyrropus

OTHER NAMES Red-legged Rope Squirrel.
Fr. *Funisciure à pattes rousses*. Ger. *Rotfussiges Baumhörnchen*.
MEASUREMENTS HB 135–266mm. T 100–200mm. W 160–300g.
RECOGNITION A velvety-furred squirrel with rich rufous limbs and face, and a dark (sometimes almost black) back, finely flecked with pale buff to give it a greenish appearance. The underside is white, sometimes orange. A pale side-stripe on the flanks is a variable feature (as is the intensity of red in the tail and limbs). Tail hair bases are orange, then black with white tips, giving a silvery 'halo'. Often heard before it is seen, this species utters a series of strident, bird-like chirps and a loud three-syllable call.
HABITAT From Sierra Leone to the R. Nile and throughout the Congo R. basin at low and medium altitudes. It prefers undergrowth and especially palm groves under a closed canopy. Nests are generally made at low level, especially among buttress roots.
FOOD In Gabon, about 75% fruits, 18% animal matter. Gums and mushrooms are also eaten regularly. Forages mostly on the ground.
STATUS Common and widespread.

KINTAMPO ROPE SQUIRREL

Funisciurus substriatus

OTHER NAMES Fr. *Funisciure du Kintampo*. Ger. *Kintampo Baumhörnchen (Togostreifenhörnchen)*.
MEASUREMENTS HB 150–180mm. T 140–200mm. W (est.) 100–150g.
RECOGNITION A small, olive-coloured squirrel with short, poorly defined light and dark stripes on the flanks. Tail hairs are grey at the base then dark brown with buff tips, giving a pattern of muted bands from above and a pale longitudinal strip from the side.
HABITAT Woodlands and forest edges in the 'Dahomey Gap' area between Nigeria and Ghana.



Kintampo Rope Squirrel

FOOD Not recorded.
STATUS Dense settlement and cultivation coupled with a scarcity of records from its area of distribution suggest that this is a rare or vulnerable species.

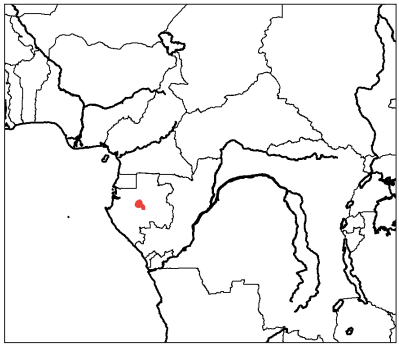
Du Chaillu's Rope Squirrel

Kintampo Rope Squirrel

DU CHAILLU'S ROPE SQUIRREL

Funisciurus duchaillui

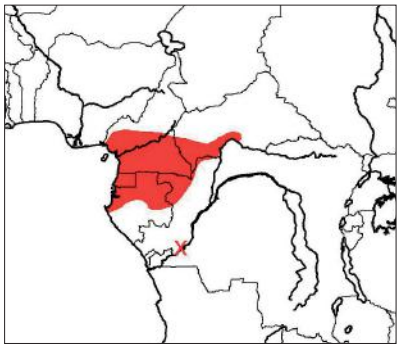
OTHER NAMES Fr. *Funisciure de Duchaillu.* Ger. *Duchailluu Baumhörnchen.*
MEASUREMENTS HB 185–212mm. T 190–230mm. W 180–220g.
RECOGNITION Olive-brown with light-grey underside and two white stripes on either side of a black mid-dorsal stripe. Formerly regarded as a subspecies of *F. isabella*.
HABITAT Forest dominated by leguminous trees. Primarily arboreal.
FOOD Fruit (*Dialium* and *Xylopia* noted).
STATUS Not yet evaluated.


Du Chaillu's Rope Squirrel

LADY BURTON'S ROPE SQUIRREL

Funisciurus isabella

OTHER NAMES Fr. *Funisciure de Gray.* Ger. *Lady Burtons Baumhörnchen.*
MEASUREMENTS HB 143–170mm. T 130–180mm. W 90–140g.
RECOGNITION A small, dark squirrel with pale stripes delimiting four bold black stripes running from head to tail. The head and outer limb surfaces are olive-brown and the underside pale grey. Tail hairs are

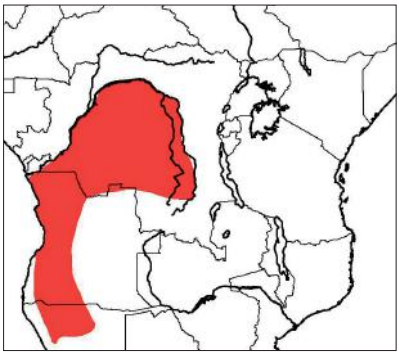

Lady Burton's Rope Squirrel

relatively short and are banded in ochre and black, giving the appearance of warm flashes along its entire length.
HABITAT Occurs patchily between the Congo R. and R. Cross in Gabon, lower Cameroon and in montane forest in the Highlands. Woven nests, in the form of a complete globe, are sealed when occupied by the young.
FOOD In Gabon, fruits (80%) and leaves (about 10%). Small amounts of animal matter and occasionally mushrooms are also taken.
STATUS Patchy distribution. IUCN rates as of least concern.

CONGO ROPE SQUIRREL

Funisciurus congicus

OTHER NAMES Striped Tree Squirrel. Fr. *Funisciure de Kuhl*. Ger. *Kongo Baumhörnchen*.
MEASUREMENTS HB 142–168mm. T 153–190mm. W 108–113g.
RECOGNITION The back is grizzled brown, with a long white side-stripe and a narrower dark line below it. Outer surfaces of the limbs, flanks and face are buff. The underside and eye-ring are white or pale. The long tail has distinct bars and a yellowish 'halo'. A very vocal species, often seen in groups numbering up to four.
HABITAT Ranges over a large part of the Congo basin and W Angola, occupying diverse habitats, from isolated belts of large trees growing in very dry savannas to true rainforest.
FOOD Spends about half of its time on the ground, foraging for fallen seeds and fruit of dominant tree or shrub species, such as Mopane (*Colophospermum mopane*), *Commiphora* and *Grewia*. It is also an agile climber after leaves and shoots of *Justicia* and leaf galls. Caterpillars are also eaten. In N Namibia optimal feeding may influence two birth peaks (just before and after the wet season).
STATUS Widespread and common.



Congo Rope Squirrel

BUSH SQUIRRELS *Paraxerus*

Alexander's Bush Squirrel	*Paraxerus alexandri*
Cooper's Mountain Squirrel	*Paraxerus cooperi*
Green Bush Squirrel	*Paraxerus poensis*
Böhm's Bush Squirrel	*Paraxerus boehmi*
Striped Bush Squirrel	*Paraxerus flavovittis*
Ochre Bush Squirrel	*Paraxerus ochraceus*
Smith's Bush Squirrel	*Paraxerus cepapi*
Tanganyika mountain squirrels	*Paraxerus (lucifer)* group
Vincent's Bush Squirrel	*Paraxerus vincenti*
Red-bellied Bush Squirrel	*Paraxerus palliatus*

RECOGNITION Short, thick fur, very variable (and sometimes bright) colour patterns and a tendency to slightly longer ear pinnae are typical features of bush squirrels. A large, diverse and adaptable group, closely related to rope squirrels, but more heterogenous, including both very small and quite large species. Most species have three pairs of mammae.
GENEALOGY There appear to be four main groups; the dwarfed *P. alexandri*, a much larger-bodied

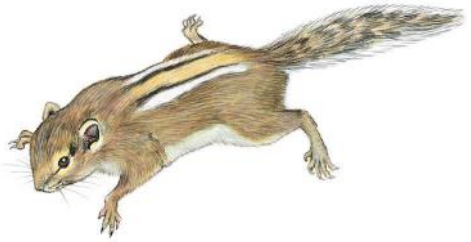
East African coast and mountain cluster and diverse small squirrels that have eastern and western wings.

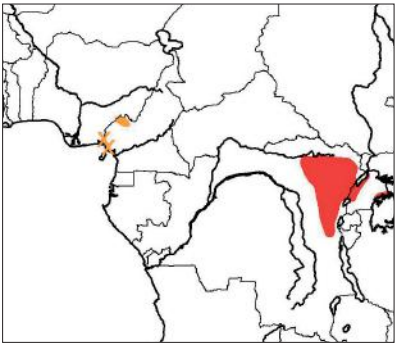
GEOGRAPHY Predominantly East and Central African (in contrast to the rope squirrels' preference for equatorial rainforests). Some species appear to be at an advantage in climatically unstable areas. As a group they span a wide range of ecotypes.

ECOLOGY Some are eastern ecological equivalents of rope squirrel species in West Africa and show a preference for low-level vegetation and shade, some spending much time on the ground. Very varied diets include fruits, seeds, nuts, mushrooms, gum and invertebrates.

NATURAL HISTORY Unlike sun squirrels, which are fast arboreal 'fleers', bush squirrels tend to be 'hiders' and, in the face of a potential threat, will slide or creep out of sight, hugging themselves close to a branch.

ADAPTATIONS Bush squirrels have robust, well-cusped teeth with hard enamel, well suited to varied and omnivorous diets.





ALEXANDER'S BUSH SQUIRREL

Paraxerus alexandri

OTHER NAMES Fr. *Ecureuil de brousse d'Alexandre*. Ger. *Alexander Buschhörnchen*.

MEASUREMENTS HB 90–120mm. T 110–145mm. W 37–72g.

RECOGNITION Very small, greenish squirrel with white ears and a medial tawny-yellow stripe flanked by thin dark and light stripes from shoulder to rump. The tapered tail is thinly haired, with indistinct, irregular ochre and dark brown barring.

HABITAT Strictly equatorial lowland forests (below 1,500m), from the eastern bank of the R. Lualaba to the R. Nile in Uganda. Prefers to hunt over the surfaces of the thick limbs of large trees.

FOOD Insects, resin, micro-flora and plant matter.

STATUS Locally common but declining due to felling of primary forest.

COOPER'S MOUNTAIN SQUIRREL *Paraxerus cooperi*

OTHER NAMES Cooper's Bush Squirrel. Fr. *Ecureuil des bois de Cooper*. Ger. *Cooper Buschhörnchen*.

MEASUREMENTS HB 190–200mm. T 190mm. W (est.) 200–300g.

RECOGNITION The back is grizzled olive-green and the underparts are pale grey mixed with a yellowish sheen. Cheeks are yellowish. The long, slender but bushy tail has narrow ochre stripes between broader brown bars. Hands, feet and thighs are of variable colour, sometimes deep russet.

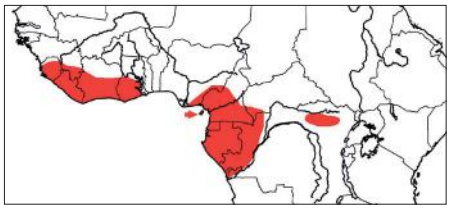
HABITAT Montane and intermediate forests in the Cameroon highland area.

FOOD Fruits and flowers of the tallow tree (*Pentadesma*) have been noted.

STATUS Highly localised in habitats subject to rapid destruction. Vulnerable, although locally common.

GREEN BUSH SQUIRREL

Paraxerus poensis



Green Bush Squirrel

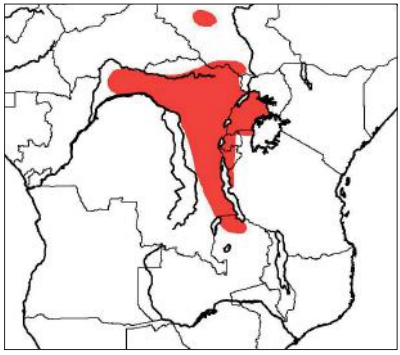
OTHER NAMES Fr. *Petit Ecureuil de brousse*. Ger. *Grünes Buschhörnchen*.
MEASUREMENTS HB 140–180mm. T 140–190mm. W 90–150g.
RECOGNITION A small, grizzled green squirrel with a yellow belly, grey chest and grizzled black tail.
HABITAT Forest and forest fringes with a marked preference for secondary growth, oil palms and cultivation mosaics (in the west) and for rainforest canopy (in the east). Ranges from Sierra Leone to the R. Ubangi and Congo R.
FOOD In Gabon, palm husks, palm kernels and fruits (90%), animal matter (10%).
STATUS Not endangered.

Green Bush Squirrel

Böhm's Bush Squirrel

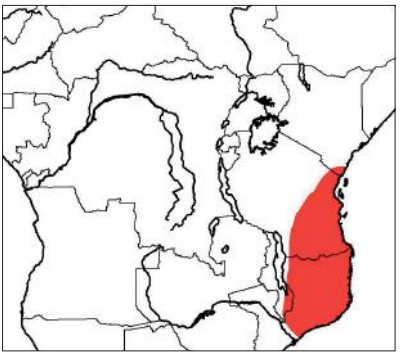
BÖHM'S BUSH SQUIRREL

Paraxerus boehmi



Böhm's Bush Squirrel

OTHER NAMES Fr. *Ecureuil de brousse de Boehm*. Ger. *Bohm Buschhörnchen*.
MEASUREMENTS HB 100–150m. T 90–200mm. W 40–100g.
RECOGNITION A small, olive-coloured squirrel with a yellowish dorsal stripe and conspicuous pale flank-stripes in between bold black stripes running from shoulder to rump. The tail is distinctly barred in dark brown and cream. The underside is off-white.
GEOGRAPHIC VARIATION *P. b. boehmi* (N, E and S DR Congo): dark olive. *P. b. emini* (east of Rift, Uganda): light olive. *P. b. vulcanorum* (Rwenzori, Kivu): russet tints.
HABITAT Undergrowth and liana tangles in mixed, swamp, lowland and montane forests. Also (marginally), in wooded savannas from Congo R. eastwards to the R. Nile and L. Victoria. This species appears to be the eastern ecological equivalent of the Ribboned Rope Squirrel (*Funisciurus lemniscatus*).
FOOD Insects and resinous gums, mushrooms, fruits and seeds.
STATUS Locally common.



Striped Bush Squirrel

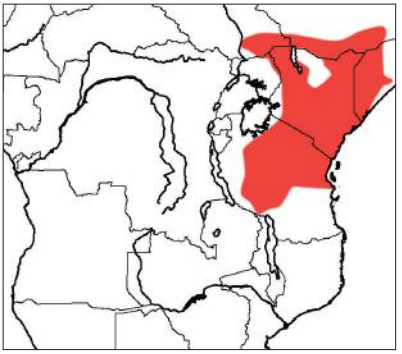
STRIPED BUSH SQUIRREL

Paraxerus flavovittis

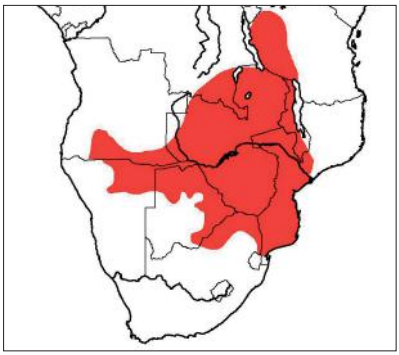
OTHER NAMES Fr. *Ecureuil de brousse rayé*.
Ger. *Streifen Buschhörnchen*.
MEASUREMENTS HB 160–200mm. T 140–180mm. W (est.) 120–200g.
RECOGNITION Medium-sized to small, grizzled squirrel with a white stripe down the side emphasised by dark lines above and below. The face also has indistinct 'bands' across the cheek and eye regions. The tail is indistinctly marked with irregular bars. The pale feet have large, heavily clawed toes.
HABITAT Savanna, forest, thicket and cultivated land, with a marked preference for groves of sugar plum (*Uapaca*) trees. Ranges from Zambezi east of L. Malawi (L. Nyasa) to the Tanzania coast.
FOOD Fruits, seeds, buds, leaves and roots. Feeds on the ground and in trees.
STATUS Probably declining in some areas but not endangered.

OCHRE BUSH SQUIRREL *Paraxerus ochraceus*

OTHER NAMES Fr. *Ecureuil de brousse ocre*. Ger. *Ocker Buschhörnchen*.
MEASUREMENTS HB 130–185mm. T 130–190mm. W 80–100g.
RECOGNITION Very variable, grizzled squirrel, with a pale off-white to yellow ochre underside. Subdesertic forms are very pallid; montane populations have darker olive backs. The tail has fine, irregular barring.
HABITAT Dry forests and thickets at various altitudes; also, wooded riverine strips in very arid country from South Sudan to E African coast as far south as R. Rufiji.
FOOD Fruits, seeds, buds, flowers, roots, bulbs, acacia gum. Occasionally some animal foods.
STATUS Abundant and widespread.



Ochre Bush Squirrel



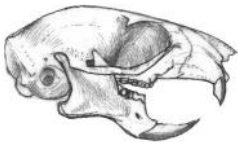
Smith's Bush Squirrel

SMITH'S BUSH SQUIRREL

Paraxerus cepapi

OTHER NAMES Fr. *Ecureuil de brousse de Smith*. Ger. *Ockerfuss Buschhörnchen*.
MEASUREMENTS HB 130–185mm. T 120–180mm. W 100–260g.
RECOGNITION Pale grizzled squirrel of very variable tints. Yellowish tints on the face, hindquarters and shoulders may be localised or more extensive. Underparts are white or yellowish. The tail is grizzled, with indistinct black bars and a broken pale-tipped 'halo'. Note: It is possible that this species hybridises with *P. palliatus* in Mozambique.
HABITAT Miombo (*Brachystegia*) woodlands and associated woods and thickets from Angola to W Tanzania and Mozambique.
FOOD Various plant foods and insects.
STATUS Abundant and widespread.

TANGANYIKA MOUNTAIN SQUIRRELS *Paraxerus (lucifer)* group



There are three, perhaps four, separate populations of closely related Tanganyika mountain squirrels. All have soft fur with warm tints on the face, feet and base of the tail and silvery-tipped dove-grey undersides. In *P. (l.) byatti* the tints are muted, the back is grizzled olive and the tail is barred with dark brown and fine cream cross-bars. In the Usambara Mts some squirrels can be virtually indistinguishable from *P. (l.) byatti* but some sport orange tail-tips, bright orange limbs and muzzles. This morph, generally identified as *P. (l.) vexillarius*, and only known from the Usambaras (which are entirely surrounded by lowland *P. palliatus*), strongly suggests that hybridisation between *P. (l.) byatti* and *P. palliatus* has taken place in the past (a situation that invites genetic research to settle species allocations in this group). In the larger *P. (l.) laetus* the face, limbs and rump region are more strongly russet and the tail is more thickly haired with bold black-and-white bars. *P. (l.) lucifer* is richly red all over, with a black back and half-hidden black bars in the thick red tail. *P. (l.) byatti)* is found in montane forests of E Tanzania, *P. (l.) laetus* on the eastern side of L. Malawi (L. Nyasa) and *P. (l.) lucifer* north and west of L. Malawi. This group of squirrels has been widely misinterpreted by various authors.

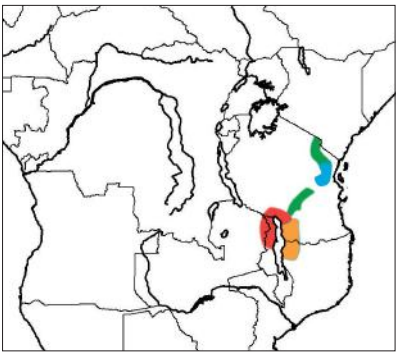
RED TANGANYIKA MOUNTAIN SQUIRREL

Paraxerus (lucifer) lucifer

OTHER NAMES Black-and-red Bush Squirrel. Fr. *Ecureuil de brousse rouge et noir*. Ger. *Tanganjika-Buschhörnchen.*
MEASUREMENTS HB 200–330mm. T 160–270m. W (est.) 650–750g.
RECOGNITION Richly red face, flanks, limbs and tail, dove-grey belly and throat, black back and half-hidden black bars in the thick red tail.

Red Tanganyika Mountain Squirrel

Kipengere Mountain Squirrel



Tanganyika mountain squirrels

Red Tanganyika Mountain Squirrel
Kipengere Mountain Squirrel
Kilimanjaro Mountain Squirrel
Lushoto Mountain Squirrel

HABITAT Montane forests north and west of L. Malawi (L. Nyasa).
FOOD Fruits, nuts and invertebrates.
STATUS Vulnerable as an already fragmented range loses its highland forests to settlement. IUCN rates as data deficient.

KIPENGERE MOUNTAIN SQUIRREL *Paraxerus (lucifer) laetus*

OTHER NAMES Fr. *Ecureuil de brousse de Kipengere*. Ger. *Kipengere-Buschhörnchen*.
MEASUREMENTS HB 230–260mm. T 160–265mm. W (est.) 650–700g.
In *P. (l.) laetus* the face, limbs and rump region are more strongly russet than in *P. (l) byatti* and the tail is more thickly haired with bold black-and-white bars.
HABITAT Montane forests in the Kipengere range, on eastern side of L. Malawi (L. Nyasa) (*P. l. laetus*).
FOOD Fruits, nuts and invertebrates.
STATUS Vulnerable, especially to the fashion for converting indigenous forests to pine, pyrethrum and other plantations of exotics. Continued protection of the biologically unique highland communities of the Kipengere range is essential for the survival of this squirrel and many other local endemics.

KILIMANJARO MOUNTAIN SQUIRREL *Paraxerus (lucifer) byatti*

OTHER NAMES Fr. *Ecureuil de brousse de Byatt*. Ger. *Byatt Buschhörnchen*.
MEASUREMENTS HB 200–240mm. T 160–215mm. W (est.) 650–750g.
RECOGNITION There are several separate populations. All have soft fur with warm tints on the face, feet and base of the tail and silvery-tipped dove-grey undersides. In *P. l. byatti* the tints are muted, the back is grizzled olive and the tail is barred with dark brown and fine cream cross-bars.
HABITAT Montane forests of E Tanzania: Kilimanjaro, Pare, Uluguru and Udzungwa.
FOOD Fruits, nuts and invertebrates.
STATUS All populations are vulnerable and totally dependent on continued protection of their now very fragmented forest relict ranges.

LUSHOTO MOUNTAIN SQUIRREL

Paraxerus (lucifer) vexillarius

OTHER NAMES Swynnerton's Bush Squirrel.
Fr. *Ecuriel de brousse de Kershaw*.
Ger. *Lushoto-Buschhörnchen*.
MEASUREMENTS HB 240mm. T 210mm.
W (est.) 650–700g.

Kilmanjaro Mountain Squirrel

Lushoto Mountain Squirrel

RECOGNITION Bright orange hands, feet (and often, tail tip), with a dark olive-green back, dove-grey belly and black-and-white barred tail.
HABITAT Confined to the montane forests of the W Usambaras, where it is in very close vicinity of *P. palliatus*. The possibility of this squirrel being the result of hybridisation (with *P. palliatus*) must be considered although it might derive from genetic drift in a very small founding stock of *P. (l) byatti* type. Genetic analysis should be able to settle this issue. It is very tentatively treated here as a full species within the Tanganyika mountain squirrel group.
FOOD Fruits and seeds.
STATUS Fragmentation of the Lushoto forests and expanding cultivation of cardamon threaten its survival. IUCN rate this (questionable) taxon as near threatened.

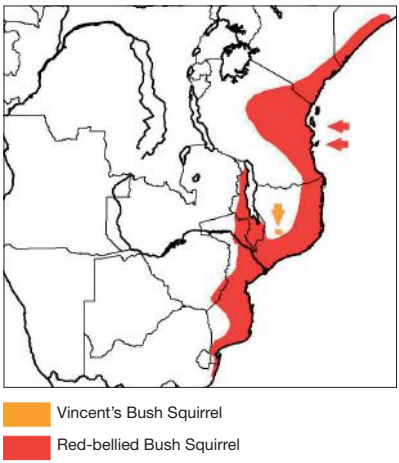
VINCENT'S BUSH SQUIRREL *Paraxerus vincenti*

OTHER NAMES Selinda Mountain Squirrel. Fr. *Ecureuil de brousse de Vincent*. Ger. *Vincents Buschhörnchen*.
MEASUREMENTS HB 206–218mm. T 120–298mm. W (est.) 200–550g.
RECOGNITION A very dark grizzled squirrel with orange limbs, underparts and face. Tail particularly dark but with orange tips to the hairs and barely perceptible orange banding.
HABITAT Only known as an isolate in montane forest on Mt Namuli.
FOOD Fruits, berries, seeds and various plant parts.
STATUS IUCN classes as endangered.

RED-BELLIED BUSH SQUIRREL

Paraxerus palliatus

OTHER NAMES Red Bush Squirrel. Fr. *Ecureuil de brousse à ventre roux*. Ger. *Rotbauchiges Buschhörnchen*.
MEASUREMENTS HB 170–250mm. T 100–270mm. W (est.) 200–550g.
RECOGNITION Pepper-and-salt grizzled squirrel with orange limbs, underparts and face. Tail hairs show variable degrees of red or orange tipping.
GEOGRAPHIC VARIATION *P. p. palliatus* (centre of range): black-and-orange tail. *P. p. tanae* (north of range): orange tail. *P. p. ornatus* (south of range): dark red and black tail. Note: Apparent intermediate individuals raise the possibility that this species hybridises with *P. cepapi* in Mozambique.
HABITAT Coastal forests and evergreen thickets, lowland riverine forests.
FOOD Fruits, berries, seeds and various plant parts.
STATUS Not endangered but *P. p. tanae* is vulnerable to forest clearance throughout its range.



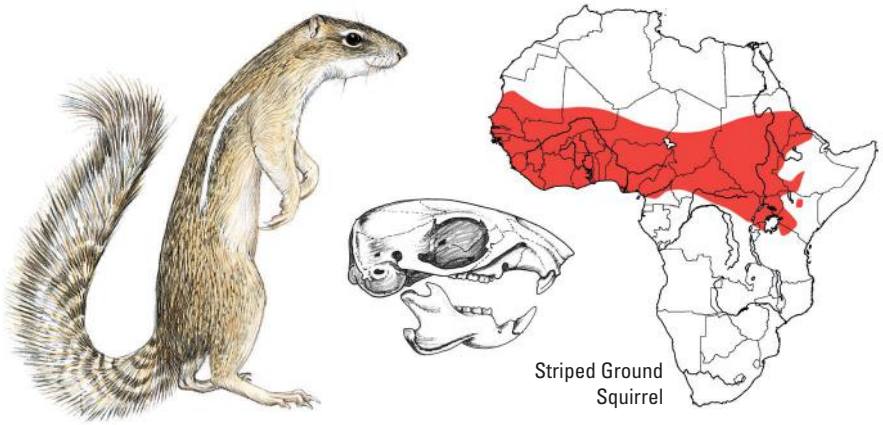
P. p. palliatus

P. p. ornatus

GROUND SQUIRRELS *Xerus*

Striped Ground Squirrel	*Xerus erythropus*
Damara Ground Squirrel	*Xerus princeps*
South African Ground Squirrel	*Xerus inauris*
Unstriped Ground Squirrel	*Xerus rutilus*
Barbary Ground Squirrel	*Xerus getulus*

Coarse-coated terrestrial squirrels, with claws adapted to digging rather than climbing. Ancestral ground squirrels are thought to have entered Africa more than 10 million years ago. Once treated as three genera, more recent molecular studies suggest a single genus *Xerus* for all African species. Ground squirrels have little or no pinnae to the ears and all rely on self-dug burrows to escape predators and extremes of climate. The young are born blind and helpless in secure burrows and take up to 2 months to become relatively independent.



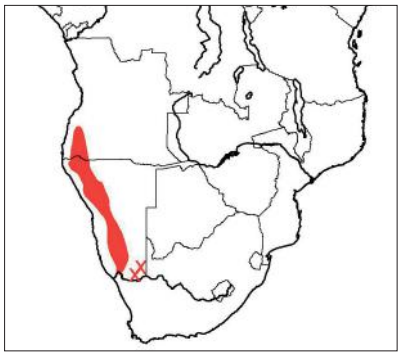
STRIPED GROUND SQUIRREL *Xerus erythropus*

OTHER NAMES West African Ground Squirrel, Geoffrey's Ground Squirrel. Fr. *Ecureuil fouisseur du Sahel*. Ger. *Gestreifetes Erdhörnchen*.
MEASUREMENTS HB 160–430mm. T 124–269mm. W 226–750g.
RECOGNITION Grizzled brown terrestrial squirrel, lighter in arid areas, darker in more humid areas. Long tail lightly banded, a single short stripe on each side. Muzzle long, blunt and well furred, with projecting nose.
HABITAT Open woodlands, Sudanic savannas and Sahelian habitats from Mauritania to E Africa. Lives in rock and tree-root crevices, termitaria and in self-dug burrows.
FOOD Roots, grass seeds, fallen fruits, seeds and nuts, *Acacia* pods, leaves and various animal foods. Nuts and seeds may be stored in burrows or crevices.
STATUS Common and widespread.

DAMARA GROUND SQUIRREL *Xerus princeps*

OTHER NAMES Mountain Ground Squirrel, Kaokoveld Ground Squirrel. Fr. *Ecuriel fouisseur du Damara*. Ger. *Damara-erdhörnchen*.
MEASUREMENTS HB 230–290mm. T 205–282mm. W 572–716g.
RECOGNITION Resembles South African Ground Squirrel *X. inauris* but has orange incisors and bushier tail, brighter and lighter colour, white side-stripe, big orbits.

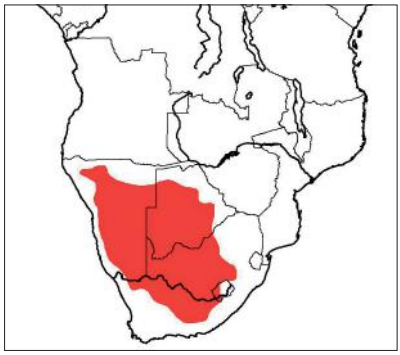
HABITAT Rocky hillsides and outcrops along the Kaokoveld escarpment from S Angola to S Namibia where it tolerates higher temperatures than *X. inauris*. Takes refuge in burrows under rocks and in crevices – avoids flat, open land.
FOOD Leaves and basal stems of grasses, roots, bulbs and tubers; also leaves, buds and fruits of bushes (notably mopane) and various insects.
STATUS Currently not endangered.



Damara Ground Squirrel

SOUTH AFRICAN GROUND SQUIRREL *Xerus inauris*

OTHER NAMES Cape Ground Squirrel. Fr. *Ecureuil fouisseur du Cap*. Ger. *Kap-erdhörnchen*.
MEASUREMENTS HB 200–300mm. T 183mm. W 500–1,100g.
RECOGNITION Tawny-yellow squirrel, bristly-haired, with a very round, blunt head and large eyes. Incisor teeth are white. The white underside is almost naked in many individuals. There is a dull white side-stripe on the flanks and two bands on the hairs of the tail. Diurnal and gregarious (with territorial groups based on a hierarchy of resident breeding females and more peripatetic males). Very vocal and playful.
HABITAT Open country in southern Africa, with a strong preference for compacted sandy areas where it digs its communal burrows. Stones and shallow scrapes around the colony entrances are regularly rubbed with the face or anal region or urinated on. Sunning and sand-bathing are regular activities. Continuous excavation makes warrens very large and complex and spreads spoil heaps all around the many exit holes. Spare burrow space is often used by mongooses (Yellow Mongooses and Suricates), which sometimes also play with the squirrels. The massive impact that the squirrel has on its immediate surroundings is also partly due to its excavation of food plants and excretion of nutrients.
FOOD Leaves and stems of grasses and shrubs, seeds, bulbs and tubers; also leaves, buds and fruits of bushes and various insects.
STATUS Not endangered.

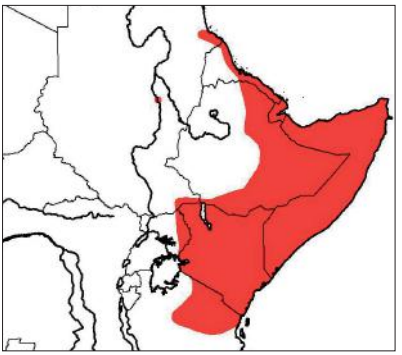


South African Ground Squirrel

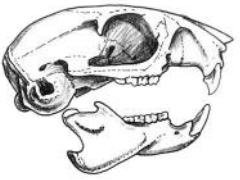
UNSTRIPED GROUND SQUIRREL

Xerus rutilus

OTHER NAMES Pallid Ground Squirrel. Fr. *Ecureuil fouisseur*. Ger. *Erdhörnchen*.
MEASUREMENTS HB 200–260mm. T 180–230mm. W 300–335g.
RECOGNITION A small, unstriped ground squirrel, ticked with white on a neutral or reddish ground, variably tinted belly, forelimbs and lower face. The tail is relatively sombre and often stained by earth.
HABITAT Very dry steppe, savanna and subdesert country in the Horn of Africa.
FOOD Roots, pods, seeds, fruits, stems, leaves and occasional insects.
STATUS Widespread.



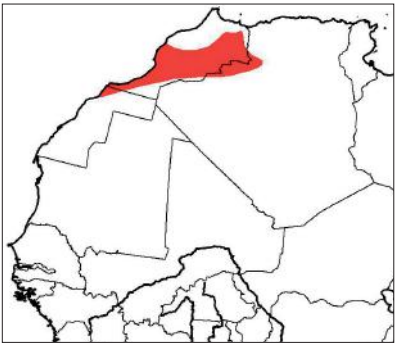
Unstriped Ground Squirrel



BARBARY GROUND SQUIRREL

Xerus (previously *Atlantoxerus*) *getulus*

OTHER NAMES Fr. *Ecureuil fouisseur de Barbarie*. Ger. *Barbarie-erdhörnchen*.
MEASUREMENTS HB (est.) 300–450mm. T (est.) 200–250mm. W (est.) 50–1,100g.
RECOGNITION A boldly striped, ground-dwelling squirrel with a short, coarse-textured coat marked with two white stripes down each side, a prominent eye-ring and a nearly naked, pale underside. The tail is bushy with bold black and white banding.
HABITAT Rocky areas with scattered trees and bushes in the Atlas Mts in Morocco and W Algeria. Diurnal, shelters in burrows or among rocks during the night and during the heat of the day.
FOOD Nuts and seeds, including those of the commercially valuable argan (*Argania*), which produces an oil used for cooking.
STATUS Widespread within its range.



Barbary Ground Squirrel

DORMICE GLIRIDAE (FORMERLY MYOXIDAE)

African dormice	*Graphiurus* (4 subgenera, 14 species)
Orchard dormice	*Eliomys* (2 species)

RECOGNITION Small, climbing rodents of nocturnal habits, intermediate in form between rats and squirrels. Once more closely allied with the former, genetic analysis has shown them to be 'pseudo-myomorphic' members of an extremely early and primitive squirrel-like lineage. They often have a prominent black 'mask' around the eyes, a bushy tail and deft fingers with very small but needle-sharp, curved claws. Their tails detach easily and the hair may regrow as a 'brush' (see p.248). The name, from the Latin *dormire*, 'to sleep', recognises their ability to become torpid when food is scarce or temperatures drop.

Graphiurus nagtaglassi

Graphiurus murinus

GENEALOGY Dormice appear as fossils at about 55 mya. They have retained a primitive, generalised gut, having no caecum for digesting cellulose. Their molar teeth are also generalised. *Graphiurus* are the least herbivorous of dormice.

GEOGRAPHY Seven genera in Eurasia and five genera/subgenera in Africa, where dormice first appear as fossils about 18 mya.

ECOLOGY Most Eurasian species lay down fat and become torpid in winter. A similar tendency is found in dormice that live in temperate regions of Africa. Dormice usually exist at relatively low densities.

NATURAL HISTORY Dormice are vocal rodents, producing audible clicks, growls and whistles, especially while mating, at which time both sexes call. An average of about three young (up to six) are born completely blind, deaf and naked in a nest that is built by the mother (who defends it vigorously against visiting dormice). The young become independent in just over 1 month.

ADAPTATIONS Generalised, omnivorous and predatory rodents with very high activity levels. Intensely exploratory and agile, mainly in trees and bushes but also on the ground, and, for three species, a marked preference for rocky habitats. Easily able to overpower animals similar in size to themselves.

Allocation of species to subgenera is still provisional and tentative.

AFRICAN DORMICE *Graphiurus*

West African Smoky Dormouse	*Graphiurus (Aethoglis) nagtaglasi*
Small-eared dormice	*Graphiurus (Claviglis)* (2 species)
African rock dormice	*Graphiurus (Gliriscus)* (3 species)
African dormice	*Graphiurus (Graphiurus)* (8 species)

WEST AFRICAN SMOKY DORMOUSE

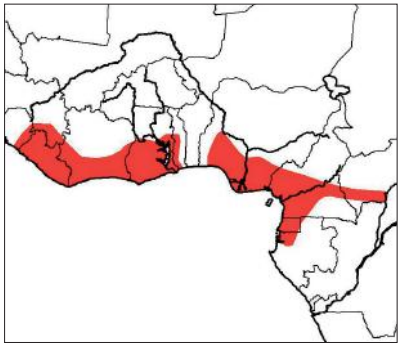
Graphiurus (Aethoglis) nagtaglasi

OTHER NAMES Nagtglas's African Dormouse. Fr. *Graphiure de Nagtaglas*. Ger. *Nagtglas Bilch.*

MEASUREMENTS HB 120–155mm. T 65–122mm. W 48–98g.

RECOGNITION The largest African dormouse, with soft, dense, grey-brown dorsal fur grading into grey on ventral surfaces variably washed with cream. Cheeks are off-white, in contrast with black eye-masks. Ears are relatively small and pointed. Genetic analysis suggests that this is the sole species deriving from the earliest glirid radiation within Africa.

DISTRIBUTION Believed to be restricted to Upper Guinea and Central West African forest regions.



West African Smoky Dormouse

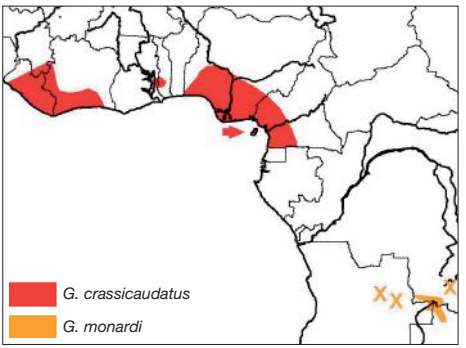
West African Smoky Dormouse

HABITAT Both primary and secondary growth, including farm-bush and banana gardens.
FOOD Arboreal foragers for both cultivated and wild fruits and for insects. Probably broadly omnivorous.
BEHAVIOUR Reportedly bolder than most dormice. Females with young have been recorded between September and April, suggesting a wet-season breeding season.
STATUS IUCN rates as of least concern.

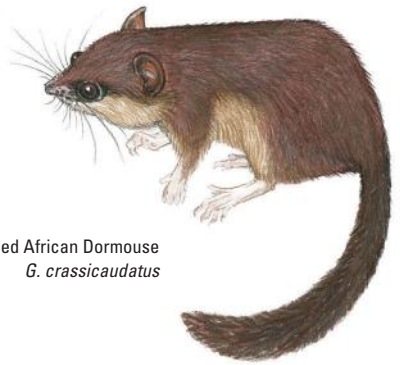
SMALL-EARED DORMICE

Graphiurus (Claviglis)

OTHER NAMES Fr. *Graphiure (Claviglis).* Ger. *Claviglis Bilch.*
MEASUREMENTS HB 83–160mm. T 55–130mm. W over 20g.
RECOGNITION Two small-eared brown dormice, *G. crassicaudatus* small (HB 92mm) and short-muzzled, *G. monardi* large (HB 160mm) and long-muzzled. Genetic analysis suggests that *G. (Claviglis)* might also derive from an early dormouse stock.
SPECIES *G. crassicaudatus*, *G. monardi.*
HABITAT *G. crassicaudatus* in both primary and secondary growth; *G. monardi* in Central African woodlands and savannas.
FOOD Fruits and insects. Probably omnivorous.
STATUS IUCN rates as data deficient.



Small-eared dormice



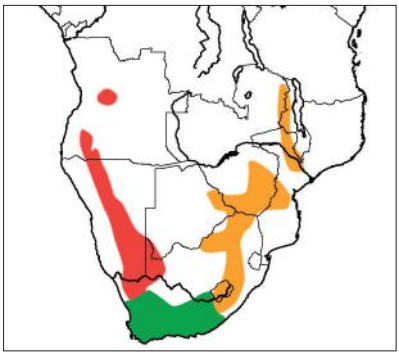
Thick-tailed African Dormouse
G. crassicaudatus

AFRICAN ROCK DORMICE *Graphiurus (Gliriscus)*

OTHER NAMES Fr. *Graphiure (Gliriscus).* Ger. *Gliriscus Bilch*
MEASUREMENTS HB 95–145mm. T 65–150mm. W 30–85g.
RECOGNITION Three small, large-eared dormice, two with somewhat flattened skulls and adapted to living among rocks with abundant crevices. All skilled climbers, grey or brown, with paler undersides, black eye-masks and furry tails.
SPECIES *G. rupicola*, *G. platyops*, *G. ocularis*.

Rupicolous African Dormouse
G. rupicola

HABITAT Southern African wooded or rocky habitats under relatively dry seasonal climates.
FOOD Seeds, green stuff and insects. Probably omnivorous.
STATUS IUCN rates as data deficient.

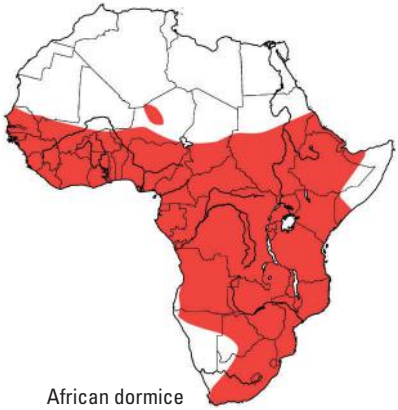


African rock dormice

AFRICAN DORMICE

Graphiurus (Graphiurus)

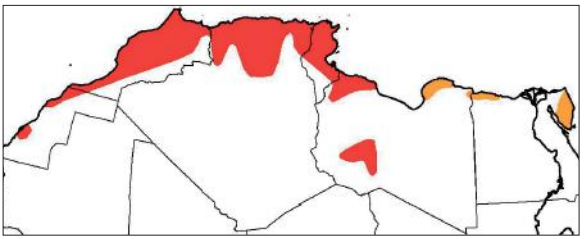
MEASUREMENTS HB 75–150mm. T 50–110mm. W 18–85g.
RECOGNITION Typified by the widespread *G. murinus* (to which all African dormice were previously allocated). *G. (Graphiurus*) are usually grey with white undersides, a dark eye-mask and prominent ears. They may also be brown or tawny. The tail is bushy and they are agile climbers, with sharp-clawed, dexterous fingers.
SPECIES *G. murinus, G. angolensis, G. christyi, G. microtis, G. johnstoni, G. kelleni* (including *G. olga* and *G. parvus*), *G. lorraineus, G. surdus*.
DISTRIBUTION Most sub-Saharan environments except open arid desert (but known as a relict in the central Saharan mountains).
HABITAT Almost all habitats but with a marked preference for dense woodlands, thickets and forests. All species make nests.
FOOD Omnivorous. Seeds, fruits, invertebrates and small vertebrates, including small birds, lizards, eggs and carrion. African dormice pounce very fast and prey may include sleeping birds, in which case deep bites are directed at the head (only the brain may be eaten).
BEHAVIOUR Some species of dormice are territorial and intolerant, but a nest of 11 adults, including animals of both sexes, has been recorded. They are very vocal and can make a loud shriek.
ADAPTATIONS Fat deposits and nest-building behaviour enable them to weather seasonal food shortages.
STATUS Many species are common; others have very local distributions. Dormice have been partially displaced as a commensal in huts and houses by the Black Rat.



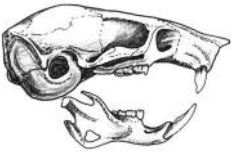
African dormice

G. (G.) murinus

E. melanurus



Orchard dormice



ORCHARD DORMICE *Eliomys*

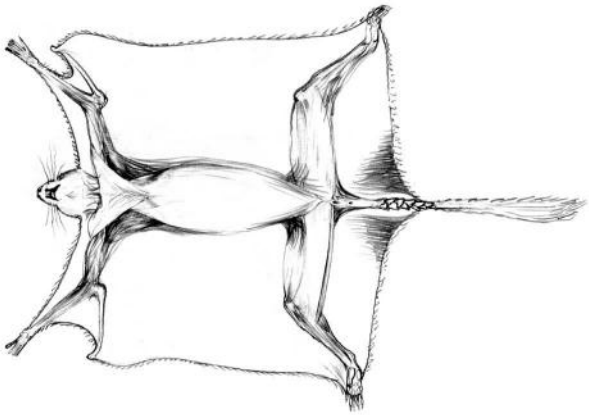
OTHER NAMES Garden dormice. Fr. *Lérot*. Ger. *Löffelbilch*.
MEASUREMENTS HB 100–170mm. T 90–150mm. W (est. ♀) 45–200g.
RECOGNITION Previously treated as a single species, the two species are best distinguished by region of origin. These are handsome dormice with a tawny forehead and a dorsal midline flanked by grey. The underparts and the base of the ear are white. Mask and jaw-line are black and there is a black brush to the tail. Often noticed because of their varied (and occasionally quite loud) vocalisations – squeaks, grunting and tooth clicking.
SPECIES *E. melanurus* in Egypt and Cyrenaica, *E. munbyanus* from the Maghreb coast and Atlas (up to 3,800m).
HABITAT All along the Mediterranean N African littoral in woodlands, date-palm oases, sand dunes and rocky country. This dormouse ranges high into treeless mountains. It may build nests in piles of natural debris or old bird's nests.
FOOD Fruits, nuts, buds, invertebrates and occasional vertebrates.
STATUS IUCN rates as of least concern.

ANOMALURES ANOMALURIDAE

Anomalures (scaly-tailed squirrels)	*Anomalurus* (4 species)
Pygmy anomalures	*Idiurus* (2 species)
Cameroon Scaly-tail	*Zenkerella insignis*

RECOGNITION Mainly gliding rodents with slender bodies concealed by long, fine fur and (in the gliders) by the gathered membrane or 'patagium'. Anomalures have narrow hands and feet with strong, bat-like claws. The tail has a short strip of two rows of spiked scales on its underside. Since these animals live on vertical surfaces, the scales help the tail to act as a rest for the body's weight and allow it to hang passively from the claws. Membranes are attached to the margins of both limbs and to a cartilaginous elbow strut. Anomalures often have a strong scent which is produced by inguinal glands that fluctuate in size.
GENEALOGY Anomalures are well represented in fossil finds dated to over 20 mya (20 genera have been identified) but anomalurid relationships to the earliest known rodents in Africa, the mid-Eocene zegdoumyids, remain likely but uncertain.

Gliding volplanes are most likely to have first evolved in response to the problems of moving between tall, isolated trees. Relatively dry, liana-free leguminous woodlands growing on leached basement surfaces are the habitats that are most likely to have provided the conditions necessary for this adaptation to develop. Contemporary equivalents of such habitats are ironwood forests and miombo (*Brachystegia*) woodlands, both of these being prime habitats for the commonest of the scaly-tails, Lord Derby's Anomalure. The success of this rodent is due to a very specific dietary staple, namely bark and bark exudates, gnawed from little over a dozen species of tree. It would appear that anomalures and their food plants have evolved together because mutually beneficial relationships have been observed between them.



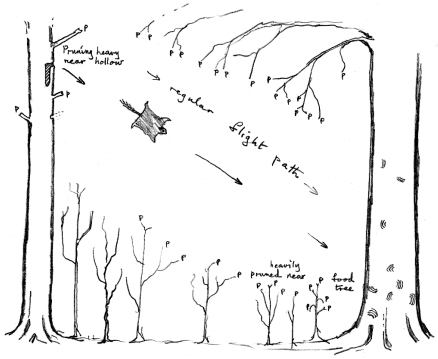
Underside of Lord Derby's Anomalure.

Anomalures, like beavers, use their incisors not only to eat bark but to cut small branches. This pruning activity can be directly correlated with habitual glide-lines radiating from dens. Dens are usually holes in vertical trunks and lateral branches growing from such trunks can be obstructing. Removal of leaf-bearing branches below a closed canopy causes 'die-back' which, in some species, opens a shallow hole in the main trunk. Such cavities are easily enlarged by anomalures, which suggests that their branch-cutting behaviour may provide additional benefits. Anomalures are also known to cut the tops off young trees growing near the bases of food trees. Persistent pruning of competitors by anomalures may provide food trees with a distinct advantage.

GEOGRAPHY At least five known food trees, miombo (*Brachystegia*), awoura (*Julbernardia*), ironwoods (*Cynometra*), owala oil trees (*Pentaclethra*) and velvet tamarinds (*Dialium*), are leguminous Caesalpinaceae. The distribution of anomalures corresponds very closely with the distribution of this group of trees, which is a major component of tropical African woodlands and forests.

ECOLOGY Tall trees with relatively vertical stems, a clear subcanopy layer, an abundance of den holes and trees with edible bark are all necessary conditions for Lord Derby's Anomalure. Other species may not share all the same requirements but close interdependencies between animal and tree are probably vital factors in the existence of all anomalure species. This family may be more precariously dependent on a specific ecology than has previously been realised. Significantly, all the food-tree species listed above are valued for their timber. Hornbills compete for their nest-holes.

NATURAL HISTORY Anomalures have excellent bifocal sight, very acute (possibly ultrasonically sensitive) hearing and depend on sound and scents for communication. Up to three precocious young, with open eyes and thick fur, are born in a hollow. Fed from the female's rather long pectoral nipples, they grow fast. They are weaned on chewed food from the parent's cheek pouches.



Left: diagram of pruned flight path.
Above: Lord Derby's Anomalure.

ADAPTATIONS Almost half the weight and much of the volume of a large anomalure is taken up by its digestive tract. Thus, to compensate for the relatively low-energy diet, the remaining tissues, such as bones, hair and skin, are models of economy in combining tensile strength with very light weight.

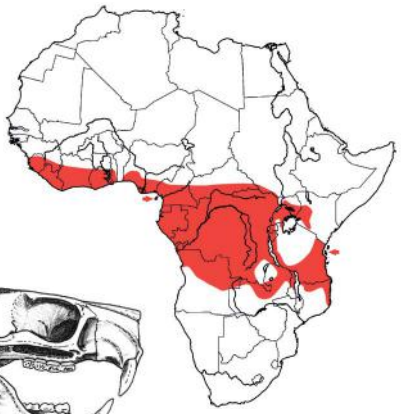
LORD DERBY'S ANOMALURE

Anomalurus derbianus

OTHER NAMES Lord Derby's Scaly-tailed Squirrel. Fr. *Anomalure de Derby*. Ger. *Derbys Dornschwanz-hörnchen*.

MEASUREMENTS HB 270–380mm. T 220–320mm. W 450–1,100g.

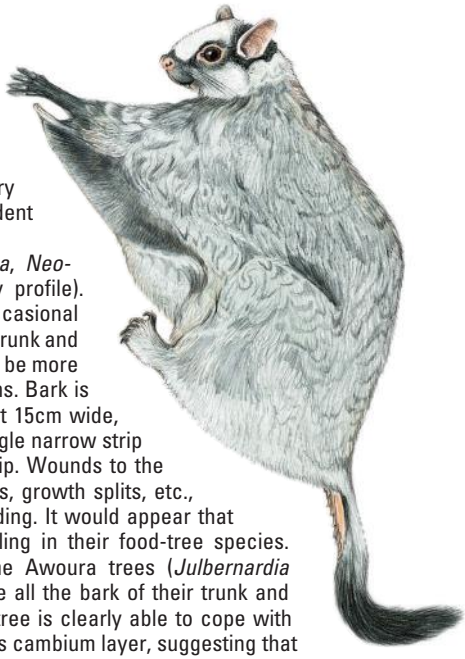
RECOGNITION Predominantly grey or brown, with a rippling silvery grizzle to the tips of the very long, fine textured fur. The membranes, which stretch between limbs and onto the root of the tail, are similarly coloured above but black bristle hairs reinforce the hem of the membrane behind the elbow strut. Colours vary greatly and 16 subspecies have been named. The main variation is in the grey or russet tints on the back and shoulders. The face is relatively short and round. The naked pinkish ears are set in a surrounding bed of dense velvet-black fur. Bristles covering the hindclaws are black.



Lord Derby's Anomalure

DISTRIBUTION From Sierra Leone to W Kenya and, more inconsistently, from N Angola to Tanzania (and probably N Mozambique). Ranges from sea level up to 2,400m.

HABITAT Moist rainforests to relatively dry woodlands at various altitudes; probably dependent upon the presence of abundant food trees.



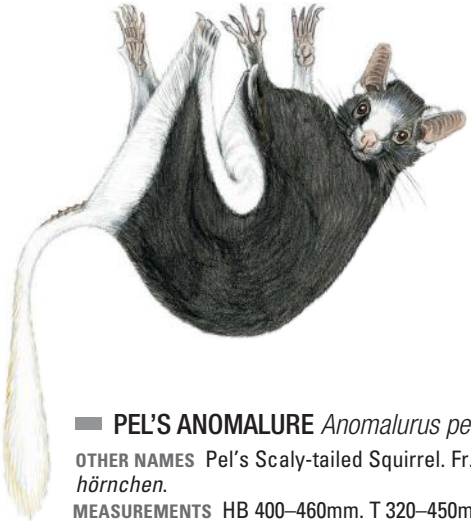
FOOD Staple is bark (of *Strombosia*, *Klainedoxa*, *Neoboutonia* and species mentioned in the family profile). In addition, fruits, flowers, leaves, nuts and occasional insects have been recorded. Thick bark from the trunk and main branches is preferred and feeding seems to be more concentrated at lower levels during drier seasons. Bark is gnawed at numerous separate sites, each about 15cm wide, which are maintained by nightly removal of a single narrow strip immediately adjacent to the previous night's strip. Wounds to the bark, caused by falling branches, elephant tusks, growth splits, etc., very often become the focus for anomalure feeding. It would appear that anomalures exploit the physiology of bark-healing in their food-tree species. As a consequence of anomalure activity some Awoura trees (*Julbernardia pellegriniana*) may, over a number of years, lose all the bark of their trunk and main branches (possibly more than once). The tree is clearly able to cope with this decortication and is able rapidly to regrow its cambium layer, suggesting that rodent and tree have co-evolved.

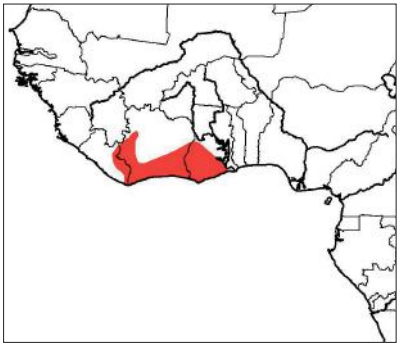
BEHAVIOUR Up to eight individuals may share a denning tree but little is known about their social behaviour. Lord Derby's Anomalure is nocturnal and lives in vertical hollow tree trunks with exit holes or cracks up to 40m up (in some woodlands they may occupy empty bee-hives). Individuals retain use of their dens over very long periods, although seasonal shifts have been recorded. Breeding is likely to be seasonal in drier areas but not in the main forest block. In some areas females are known to segregate to give birth and rear young. Apart from a threatening or

defensive hiss and growl this species also purrs and twitters. The animals like to sunbathe in the early mornings and more rarely in the evenings.

ADAPTATIONS In closed-canopy forest the pruning described in the family profile is often less frequent or less conspicuous than in more open or sun-lit areas. Where light breaks through close to a food tree, intensified pruning of young trees may serve to help maintain access to a ready food supply by killing or maiming competing trees and keeping flight-paths open.

STATUS Although localised populations are in decline from logging and forest clearance, this common and widespread species is not endangered.





Pel's Anomalure

PEL'S ANOMALURE *Anomalurus peli*

OTHER NAMES Pel's Scaly-tailed Squirrel. Fr. *Anomalure de Pel*. Ger. *Pels Dornschwanzhörnchen*.

MEASUREMENTS HB 400–460mm. T 320–450mm. W 1.3kg–1.8kg.

RECOGNITION A large anomalure with a black back and face vividly outlined with pure-white borders around the ears and on the muzzle. The underside and tail are also white, as are the borders to the flight membranes. Like Lord Derby's Anomalure, Pel's Anomalure also has six pairs of pointed scales on the underside of the tail (particularly robust in this species).

DISTRIBUTION Liberia to Ghana.

HABITAT Moist high forests with numerous tall emergents and palm trees.

FOOD Bark supplemented by fruits (especially oil and other palm dates), leaves and flowers.

BEHAVIOUR Up to six animals are known to share a den. This species is wholly nocturnal and emerges well after sunset. Contact calls have been described as deep hoots. Up to three young are born at a time and two litters a year have been recorded.

ADAPTATIONS When disturbed in its den Pel's Anomalure growls, hisses and snaps its teeth (noises that are amplified in a hole). This behaviour may deter birds of prey, primates and small carnivores, as well as hornbills (which may compete for nest-holes). Its bold colouring suggests that aggressiveness and large size may make it less vulnerable to predation than the smaller anomalure species.

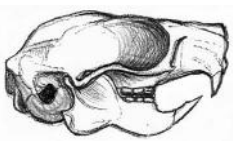
STATUS Endangered in all logged areas of its range. IUCN former assessment as near threatened is now rated as data deficient.

LESSER ANOMALURE *Anomalurus pusillus*

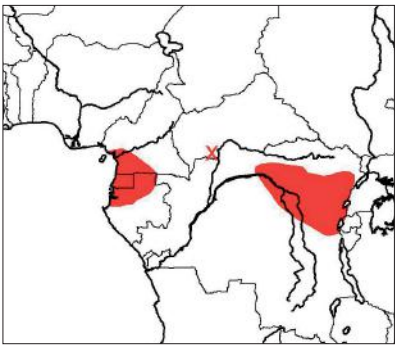
OTHER NAMES Dwarf Scaly-tailed Squirrel. Fr. *Ecureuil volant pygmée*. Ger. *Zwergdornschwanzhörnchen*.

MEASUREMENTS HB 185–246mm. T 138–200mm. W (est.) 160–300g.

RECOGNITION A small anomalure with back coloration varying from near black to mottled tan. The membrane adjoining the tail is usually yellower while the lateral membranes are dark grey. The head is grey without borders around the ears. The underside has a yellowish tinge, as do the bristles covering the hindclaws.



Lesser Anomalure



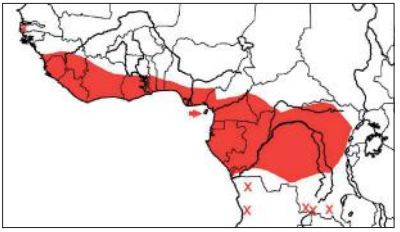
Lesser Anomalure

HABITAT A rare and probably very localised species, especially west of Cameroon. Its range may just include W Uganda but it has a strictly equatorial, non-montane distribution. Has been found sheltering in hollow trees in lowland rainforest.
FOOD Probably bark and fruits. The drupes of parasol trees (*Musanga*) have been recorded.
STATUS Rare everywhere. Biology unknown. Data deficient for assessing status.

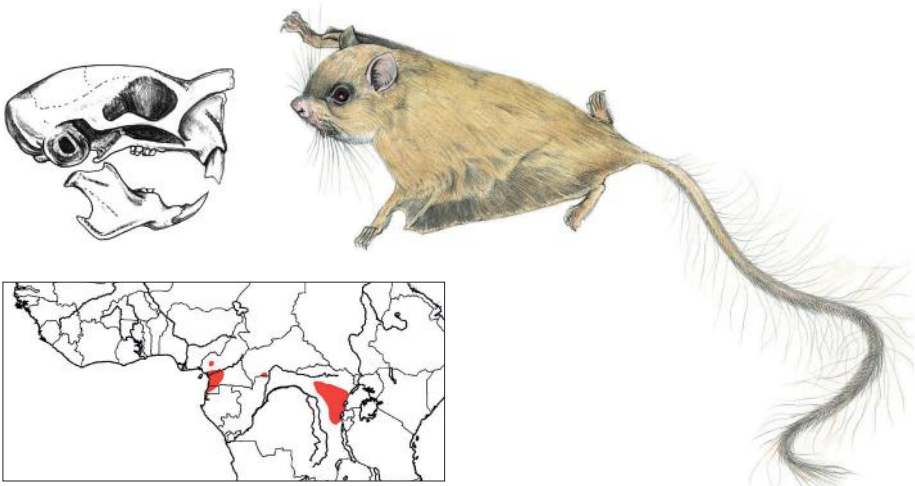
BEECROFT'S ANOMALURE

Anomalurus beecrofti

OTHER NAMES Beecroft's Scaly-tailed Squirrel. Fr. *Anomalure de Beecroft*. Ger. *Beecrofts Dornschwanzhörnchen*.
MEASUREMENTS HB 250–310mm. T 160–240mm. W (est.) 640–660g.
RECOGNITION A very variably coloured anomalure with a prominent, narrow snout. The underside is always yellow-orange to some degree and similar warm tints occur on the back in some populations, notably almost wholly orange individuals (formerly distinguished as *A. b. fulgens* in Gabon). Beecroft's Anomalure often has a white spot on the forehead but does not have a dark 'mask' around the eyes. The tail, which is narrower than in other species, has up to nine pairs of scales on its underside.
HABITAT Tropical rainforests from Sierra Leone to E DR Congo, from sea level up to 2,500m. Beecroft's Anomalure shows a marked preference for palm groves and can withstand some cultivation and plantation in its habitat if palms and some big trees remain. It rests up in holes and will also hide in the junctions between palm fronds or cling to the sheltered underside of major tree branches close to the trunk.
FOOD Fruits, especially palm dates, bark, leaves and occasional insects.
STATUS Declining locally but widespread.



Beecroft's Anomalure



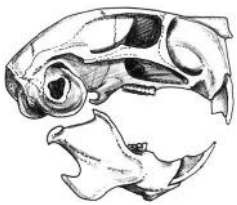
Zenker's Flying Mouse

ZENKER'S FLYING MOUSE *Idiurus zenkeri*

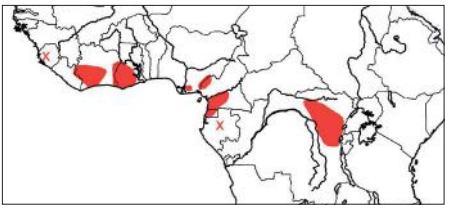
OTHER NAMES Zenker's Pygmy Anomalure, Pygmy Scaly-tailed Flying Squirrel. Fr. *Anomalure nain de Zenker*. Ger. *Zenkers Gleitbilch*.
MEASUREMENTS HB 63–75mm. T 83–104mm. W 14–17.5g.
RECOGNITION A miniature anomalure resembling a very silky-furred, tawny-coloured, snub-nosed mouse, with a membrane like those of the larger anomalures. The very long tail is fringed on the underside by two rows of short stiff hairs. Sparse, very long hairs on the upperside of the tail. It utters a shrill mouse-like squeak and is a very efficient, fast and agile glider.
HABITAT Very moist equatorial rainforests, from Cameroon to the Congo R. and between the R. Aruwimi and Congo R. to the foothills of Rwenzori and Kivu. Roosts in hollow trees (more rarely under bark), sometimes in ones or twos but more usually in groups that may number up to 100.
FOOD Oil-palm pulp, occasional insects and possibly exudates or nectar. It has been suggested that Zenker's Flying Mouse may travel many kilometres in a night to feed. However, nothing is known of its feeding behaviour. The notched upper incisors project out of the mouth, which may mean that food access requires sharp chiselling.
STATUS Clear-felling and other logging operations in the centre of their range must be eliminating them from some areas, especially where hollow trees are deliberately felled. IUCN rates as of least concern but data are deficient.

LONG-EARED FLYING MOUSE *Idiurus macrotis*

OTHER NAMES Long-eared Pygmy Anomalure, Long-eared Scaly-tailed Flying Squirrel. Fr. *Anomalure nain à grandes oreilles*. Ger. *Grossohr-gleitbilch*.
MEASUREMENTS HB 80–110mm. T 130–190mm. W 25–35g.
RECOGNITION A small anomalure of slightly more robust build than Zenker's Flying Mouse and with darker fur. This species is pale grey in colour with a brownish sheen. The ears and the face are somewhat longer than Zenker's



and the tail is proportionately shorter, with similar short, stiff hairs on the underside. Dense, short fur covers the rest of the tail.
HABITAT Equatorial lowlands (like Zenker's). The overall range is similar but the Long-eared Flying Mouse appears to be rarer than Zenker's in the eastern part of their ranges. This species sometimes shares hollow trees with Zenker's (and with bats).
FOOD Known to gnaw and strip bark, presumably for exudates and other bark concentrates; captives eat pulp of palm nuts.
STATUS Rare and little known. IUCN rates as of least concern.

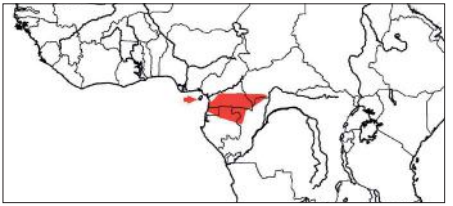


Long-eared Flying Mouse

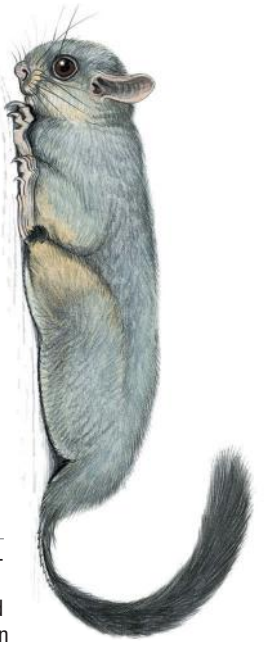
CAMEROON SCALY-TAIL

Zenkerella insignis

OTHER NAMES Cameroon Anomalure.
Fr. *Zenkerelle Anomalure aptère.*
Ger. *Kameruner Dornschwanzbilch.*
MEASUREMENTS HB 180–230mm. T 150–180mm. W (est.) 180–460g.
RECOGNITION Superficially resembling a large, big-eyed dormouse, this anomalure has no trace of a membrane (although its loose, woolly coat might cushion short, spread-eagled leaps). Head and body are a soft slate-grey with ochre tints on the forearm, lower shin and cheeks. Underparts are very pale grey and the tail is black and bushy. The strip of paired scales on the underside of the tail resembles that of other scaly-tails and implies similar 'hanging' while at rest (see above). The ankles have a brush of highly specialised 'spoon-hairs' over a glandular area. Its function and operation are not known.
HABITAT Only known from Cameroon to Gabon. Animals thought to be Cameroon Scaly-tails have been seen moving at night among low-level vines by means of very fast springy leaps. May also inhabit understorey and canopy.
FOOD Not known but certainly includes vegetable matter.
STATUS Extremely rare and status unknown. Data deficient.



Cameroon Scaly-tail



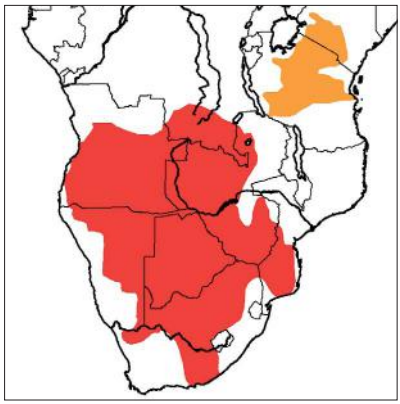
SPRINGHARES PEDETIDAE

Springhares *Pedetes* (2 species)

In spite of the many obvious differences between the gliding anomalures and the kangaroo-like springhares, both rodents probably share an ancient common ancestry; possibly among the Eocene zegdoumyid rodents. Springhares resemble many burrow-living desert rodents in having hugely enlarged inner ears, which would seem to explain their enormous sensitivity to sound and vibration.

It is remarkable that Australian kangaroos and an African rodent, both of which live on poor resources, should have evolved a mode of bouncy hopping that combines speed with great economy of energy.

SPRINGHARES *Pedetes*



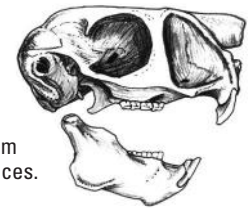
OTHER NAMES Fr. *Lièvre sauteur*. Ger. *Springhase*. Swah. *Kamendegere*.

MEASUREMENTS HB 330–460mm. T 340–490mm. W 2–4kg.

RECOGNITION Long-tailed, hopping rodents with long, soft fur, varying from warm reddish tints to yellow-grey above and white to pale tawny underneath. The brush tip of the tail and sometimes the ear tips are black. The hindlegs have four toes (most weight is carried on the enlarged third and two flanking nails). The short forelegs, often tucked out of sight, have five closely bunched, long, sharp, curved claws. The two species differ in numbers of chromosome but for all practical purposes are otherwise indistinguishable.

SPECIES Southern African Springhare *P. capensis*; East African Springhare *P. surdaster*.

DISTRIBUTION Two distinct regions of semi-arid Africa: southern and north-east. Springhares are very localised within both these areas.



HABITAT Sandy plains, pans and lake margins with well-drained soils and an extensive seasonal cover of grasses (which dry out in the long dry season). Springhares are fast and energetic diggers of burrows which may extend up to 50m, often twisting and turning haphazardly about 80cm down. Warren areas are marked by large spoil heaps near some entrances. Animals can number up to 10 per ha in relatively undisturbed habitats.

FOOD Fresh grasses, grazed to the ground, stems, roots and storage bases of grasses, new sprouts of herbs and fruits. Very occasionally insects, such as locusts, are taken. They feed only at night and within about 400m of a burrow. Up to nine animals graze in close proximity.

BEHAVIOUR Perennial breeders, the female gives birth about three times a year after a 77-day gestation. One or, more rarely, two well-developed young are fed from four pectoral teats. The young only emerge from the burrow when fully mobile and over half adult size. Springhares grunt and have a piping contact call. They bleat in distress and will bite and kick if captured. They are hunted by humans, various carnivores, eagle owls and pythons. Their burrows are used by many other animals for shelter. Springhares are able rapidly to block their burrows, and frequently do so, in order to protect themselves against attack or disturbance.

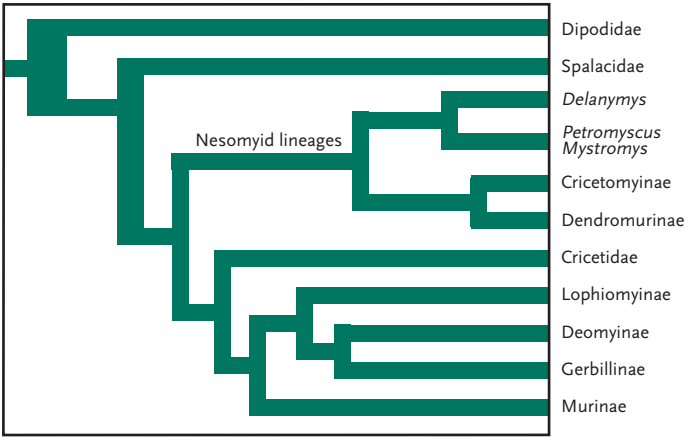
ADAPTATIONS Quick but not very manoeuvrable jumpers, they can leap up to 4m. Physiological and ecological comparisons between the two species await study.

STATUS Widespread and locally common. Heavy grazing by livestock may cause local declines. Eradicated as a crop pest in some areas, extirpated by hunting in others. Locally vulnerable but not endangered overall.

MYOMORPHA (EMBRACING MUROIDEA AND DIPODIDAE)

Myomorphs conjoin Muroidea (typified by broad, up-tilted zygomatic plates) with jerboas, Dipodidae (where zygomatic plates are narrow and nearly horizontal). The reality of this grouping, which embraces the greatest number of living rodents, has been confirmed by molecular genetics. All the rodent species that follow are myomorphs.

Tentative phylogenetic tree for the Myomorpha (mainly after Fabre *et al.* 2012)



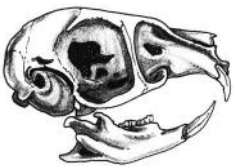
JERBOAS DIPODIDAE

Four-toed Jerboa	*Allactaga tetradactyla*
Desert jerboas	*Jaculus* (2 species)

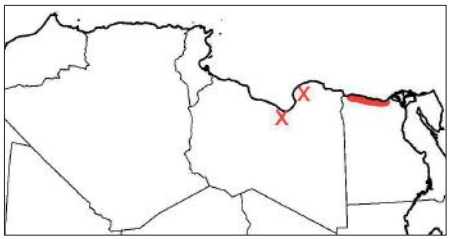
Jumping rodents with hindlegs four or more times the length of their forelegs. In spite of having small forelegs, they are efficient diggers in sandy soil (with sharp foreleg claws and teeth acting in concert at the digging face). They dig burrows that descend up to 2m below the surface. All species are nocturnal and live in arid environments, mostly in Asia, where they undoubtedly evolved. Fossils of the jerboa lineage in Eurasia go back at least 30 million years.

FOUR-TOED JERBOA *Allactaga tetradactyla*

MEASUREMENTS HB 102–119mm. T 154–180mm. W 48–56g.
RECOGNITION A mottled, sandy-coloured jerboa with four long toes, long ears and rounded head with large eyes. The long tail has a black brush terminating in a white tip. The head is disproportionally large relative to the body. Pro-odont teeth, well bedded in a wedge-shaped skull and served by muscular lips under a bulldozing snub nose are all adaptations for 'dental digging' in relatively dense, compacted soils.



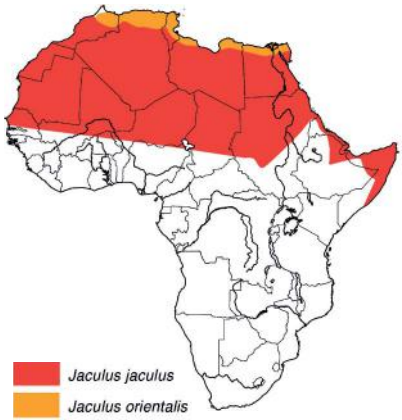
HABITAT Restricted to clays and valley soils among the gravel plains that lie between Alexandria in Egypt and the Gulf of Sirte in Libya. This essentially Asiatic genus has adapted to colder deserts and denser soils (with different specialisations, especially skull, teeth and toes, compared to sand-diggers such as the desert jerboas).
FOOD Grass seeds and roots.
STATUS Localised, rare and endangered in north Africa, notably by preferring soils suited to agriculture.

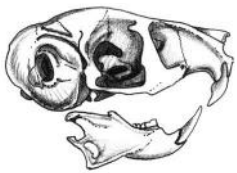


Four-toed Jerboa

DESERT JERBOAS *Jaculus*

MEASUREMENTS *J. jaculus*: HB 98–118mm. T 160–203mm. W 45–73g. *J. orientalis:* HB 137–160mm. T 195–243mm. W 108–147g.
RECOGNITION Specialised, long-legged, three-toed rodents with tawny-orange upperparts, and a white underside (and thigh stripe). The hindfeet are very elongated and hair-tufted, with toes reduced to three. The black eyes are night-adapted and very large. The nose is flat and is used to tamp the soil. While digging, the sharp-clawed, but miniscule, fore-limbs scratch tightly up below the nipping jaws (as in illustration). The very long, black and white tufted tail is often held in an elegant, button-hook curl and acts as a tripod with the hindlegs. Desert jerboas are active most of the night.
SPECIES *J. jaculus* (mainly sand dunes in the Sahara); *J. orientalis* (mainly steppe on Mediterranean littoral).
HABITAT These sand-dwelling jerboas dig deep burrows and mainly live and forage on their own but may form temporary groups of four or five in their burrows. Both species range from Mauritania to Egypt but the Three-toed Jerboa (*J. jaculus*) is the more wide-ranging and common.
FOOD Seeds, stems and roots of desert grasses.
STATUS Not endangered.





J. jaculus

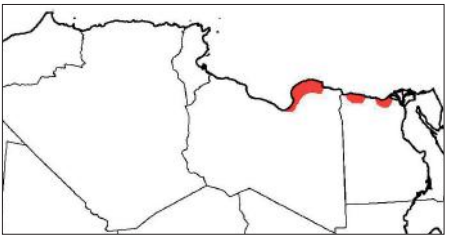
MOLE-RATS AND ROOT-RATS SPALACIDAE

Palestine Mole-rat	*Spalax ehrenbergi*
Root-rats	*Tachyoryctes* (provisionally 2 species)

Cylindrical rodents with dense fur, very short legs, minute ears, blind or much reduced eyes and a broad nose. Projecting incisors and head movements are employed in digging (the forelegs merely shuffle spoil). Abundant fossils, beginning at about 20 mya, reveal that surviving mole-rats are vestiges of a once much more diverse and widespread radiation in Eurasia that generated four subfamilies, only two of which occur in Africa. One, Spalacinae, includes the Palestine Mole-rat, which has only a marginal presence in Africa and is thought to have arrived in Egypt about 15,000 years ago. The second, Tachyoryctinae, now limited to north-eastern Africa, but formerly widespread in south-western Asia, shares origins with the South-East Asian bamboo rats, Rhyzomyinae. The earliest fossils of tachyoryctines in Africa date to little more than 2 mya, implying an older, but still relatively recent, arrival here.

PALESTINE MOLE-RAT

Spalax ehrenbergi

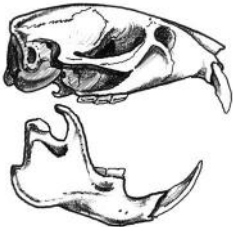


Palestine Mole-rat

OTHER NAMES Middle East Blind Mole-rat, Ehrenberg's Mole-rat.
MEASUREMENTS HB 150–270mm. T 0mm. W 130–220g.
RECOGNITION A variably coloured mole-rat with a blunt, rounded head merging into the body with no obvious neck region. Fore- and hindlegs are short and weakly clawed. The small nasal area is horny and reinforced. The most obvious signs of the mole-rat's presence are the mole hills.

HABITAT Areas of very low rainfall (absent from waterless desert) in N Egypt and Libya. Each mole-rat makes extensive burrows with a large winter breeding mound and small summer resting mounds.
FOOD Roots, bulbs, tubers and rhizomes below ground; grass, seeds.
STATUS Regarded as an agricultural pest; eliminated from commercial plantations.

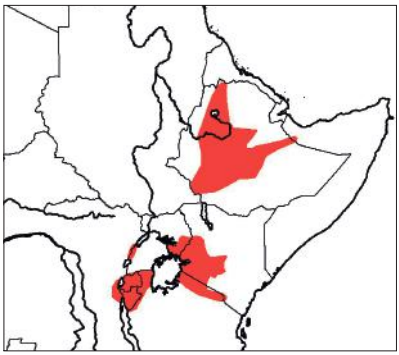
ROOT-RATS *Tachyoryctes*



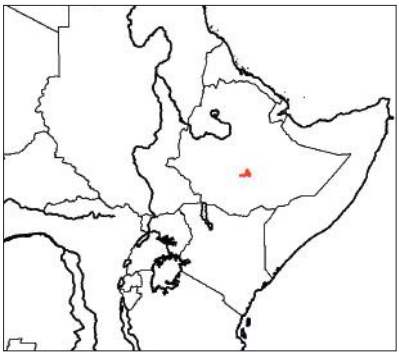
MEASUREMENTS *T. splendens*: HB 159–215mm. T 51–77mm. W 140–315g. *T. macrocephalus*: HB 224–313mm. T 40–65mm. W 330–1,000g.
RECOGNITION Chunky, subterranean, tunnelling rats with diminutive ears, small eyes and prominent orange incisors. Fur is soft, thick, russet, fawn or grey on the surface but always with a dark grey undercoat. Colouring, size and skull structure vary regionally,

Giant Root-rat, *T. macrocephalus*

African Root-rat, *T. splendens*



African Root-rat



Giant Root-rat

presumably in response to local soil conditions. Rapid diversification probably facilitated by extremely rapid breeding, high densities, discontinuous distribution and periodic fluctuations in numbers. *T. macrocephalus*, the Giant Root-rat, a very large, golden brown species, is highly distinctive. Lives at densities of 20–90 animals per ha at 3,000–4,100m above sea level. Eyes project above the forehead (mole-hill 'periscopes' presumed to allow scanning while minimising exposure). Use incisors to communicate by tapping. Strong-smelling male cheek-glands associated with male/male aggression. Male preputial glands associated with sex.

SPECIES *T. splendens*, *T. macrocephalus*. (Until recently taxonomists had listed 11 regional species.)

HABITAT Uplands (including very high-altitude afroalpine grasslands), where the root-rats make large, composting midden-mounds as well as extensive tunnels and soil heaps. Range discontinuously from Ethiopia to E DR Congo, Burundi and N Tanzania.

FOOD Various roots, tubers, stems and bulbs are indiscriminately taken underground within a short radius of the hole. Material is sorted and unwanted debris is expelled onto a large midden mound.

STATUS Current species lists are in need of revision.

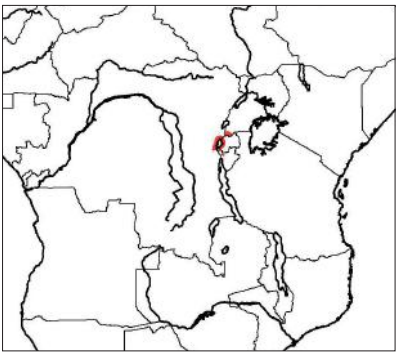
ARCHAIC MUROIDS NESOMYIDAE

It has long been known that the Nesomyidae, today's dominant rodents in Madagascar, must have derived from an early rafting from Africa. It has needed molecular genetics to explicitly link this with a disparity of African rodents that have long puzzled scientists. Early attempts to classify muroid rodents were heavily dependent on teeth or other, sometimes misleading, details of structure but molecular phylogenies have now shown that over 30 extant African species, belonging to at least 12 genera, belong to this family of archaic rodents. In Madagascar these rodents have been estimated to have begun diversifying 10.8–12.6 mya, confirming a still earlier nesomyid presence in Africa. Since that time mainland Africa has had a succession of invasions by more advanced rodents. Ensuing competition undoubtedly drove these earlier groups into ever more specialised niches.

Formerly allocated and reallocated to various, and confusing, families and subfamilies, the 12 genera that follow are here grouped under Nesomyidae. Further taxonomic subdivisions are possible and desirable but, for the purposes of this field guide, genera are clustered without further nomenclature. Nonetheless, well-recognised vernacular groupings, such as 'pouched rats' or 'climbing mice' are retained.

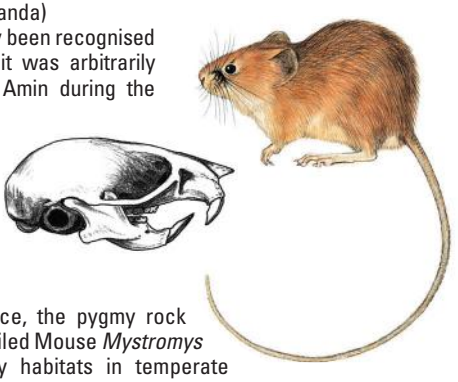
First described in 1962 and allocated to the 'climbing mice', or Dendromurinae, Delaney's Mouse *Delanymys brooksi* probably represents the sole African survivor of an extremely archaic muroid, probably nesomyid, lineage.

DELANEY'S MOUSE *Delanymys brooksi*



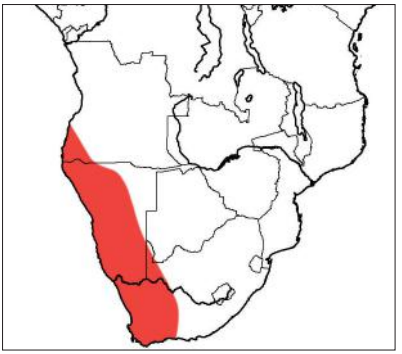
Delaney's Mouse

OTHER NAMES Delany's Swamp Mouse.
MEASUREMENTS HB 50–63mm. T 90–111mm. W 5.2–6.5g.
RECOGNITION A very small, long-tailed mouse with long hindlegs, five mobile fingers and a vestigial thumb. The dense soft hair is reddish brown interspersed with long guard hairs. There is a black spot between the eye and nostril.
HABITAT High-altitude (1,700–2,625m) marshes in E DR Congo and W Uganda, among sedges and grasses, where it builds very small, round nests.
FOOD Grass and sedge seeds (possibly unripe); captives like sorghum.
STATUS The extreme rarity and multiple endemicities of the particular swamp (Echuya, in SW Uganda) where *Delanymys* was first trapped had already been recognised (it was integral to a forest reserve), before it was arbitrarily donated, as pasture, to an associate of Idi Amin during the latter's dictatorship. The ease with which such calamities can occur illustrates the vulnerability of conservation estates under autocratic governments. In 2005 the Babaasa Report recommended national park status for Echuya. Gazetting has yet to take place. IUCN classes Delaney's Mouse as vulnerable.



Formerly described as aberrant climbing mice, the pygmy rock mice *Petromyscus* (four species) and White-tailed Mouse *Mystromys albicaudatus* are relictual rodents from dry habitats in temperate southern Africa, a refugial area for very many archaic life-forms. The 12-million-year-old Kenya fossil *Democricetodon* and later fossils from South Africa suggest that these rodent types were formerly more widespread. They are small brown or grey mice with distinctive tooth patterns.

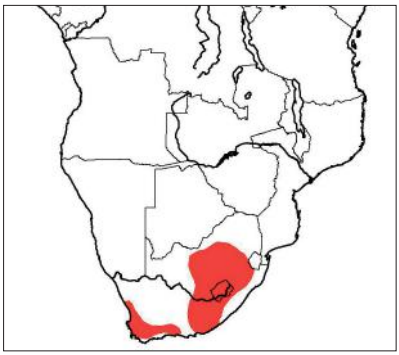
PYGMY ROCK MICE *Petromyscus*



Pygmy rock mice

MEASUREMENTS HB 75–115mm. T 75–105mm. W 17–25g.
RECOGNITION Small brown mice with broad, flattened heads and prominent ears and whiskers. The soft fur is buff or brown above, greyish below. The tail is scaly.
SPECIES *P. barbouri*, *P. collinus*, *P. monticularis*, *P. shortridgei*.
HABITAT Arid regions of SW Africa from S Angola to the Cape.
FOOD Mainly seeds.
STATUS Little known relict species.

P. collinus

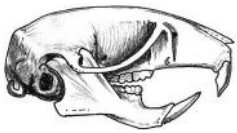


White-tailed Mouse

WHITE-TAILED MOUSE

Mystromys albicaudatus

OTHER NAMES White-tailed Rat.
MEASUREMENTS HB 105–184mm. T 50–97mm. W 75–111g.
RECOGNITION A plump, short-tailed mouse resembling a hamster, with soft grey upperparts and a white underside. The eyes are large. Incisors are yellowish and without grooves. The molar teeth are unique in their pattern of cusps and folding of enamel.
HABITAT Savanna grasslands and scrub in the southern African uplands and Cape region. Lives in crevices and burrows, where it makes a nest of shredded material.
FOOD Seeds, green vegetable matter and insects.
STATUS Poorly known.

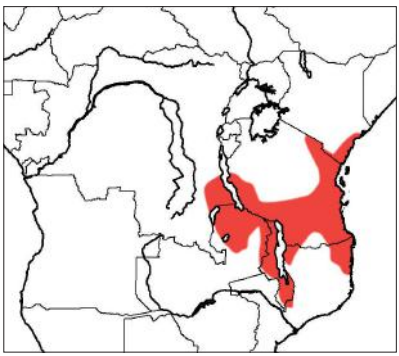


POUCHED RATS Cricetomyine nesomyids

Pouched rats have large cheek-pouches, which they fill during forays after food. All dig burrows with food-storage chambers and tend to 'camp' close to the current food source. Pouched rats are generally sluggish, grey or greyish-brown animals. The group has distinctive teeth. Genetic analysis allies the genus *Saccostomus* with the fat mice, *Steatomys*, confirming common origins among nesomyid rodents.

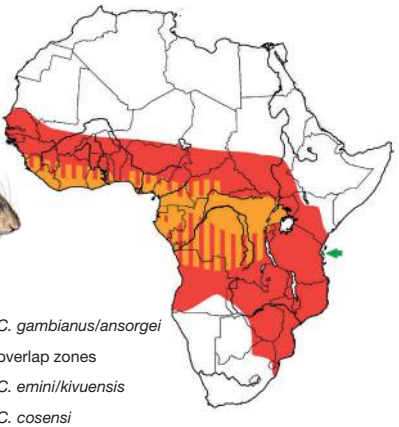
LESSER POUCHED RAT *Beamys hindei*

OTHER NAMES Long-tailed Pouched Rat.
MEASUREMENTS HB 130–187mm. T 100–155mm. W 55–150g.
RECOGNITION Small pouched rat with limp, soft fur, grey or brown upperparts, white underparts and a dark grey tail with a white tip and much mottling. A good but slow climber, it is strictly nocturnal.
GEOGRAPHIC VARIATION (sometimes treated as species): *B. h. hindei* (coastal Kenya and Tanzania), *B. h. major* (mainly montane Tanzania and Malawi).
HABITAT Sandy riverbanks in forest, thicket or dense woodland, from the Kenya coast to Malawi.
FOOD Fruits and seeds; occasionally animal foods.
STATUS Not endangered.



Lesser Pouched Rat

C. gambianus

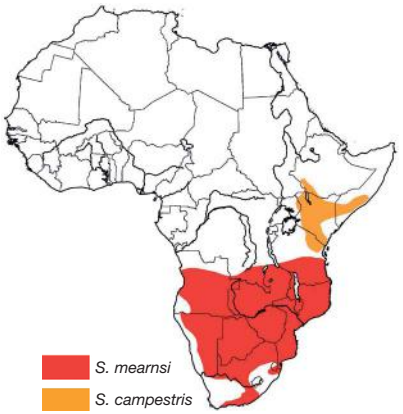


GIANT POUCHED RATS *Cricetomys*

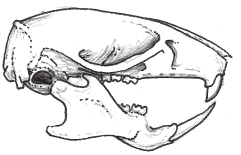
MEASUREMENTS HB 280–450mm. T 360–460mm. W 1.0–1.4kg.
RECOGNITION Large, brown or grey pouched rats, with large, naked ears. The terminal half of the long tail is white. Although sluggish, they are good climbers. They are strictly nocturnal.
SPECIES *C. gambianus* (savannas of centre–west): robust, brown, with eye-mask. *C. ansorgei* (south–east species): coarse grey-brown fur. *C. emini* (exclusively rainforest species of centre–west): gracile, short, soft grey fur. *C. cosensi* (Zanzibar). *C. kivuensis* (montane central Africa: a species primarily identified on genetic criteria – not mapped).
HABITAT Very varied (*C. gambianus*); exclusively lowland rainforest (*C. emini*).
FOOD Fruits, seeds, nuts, roots and leaves, which are collected in the cheek-pouches and taken back to the extensive burrow (where found objects, pebbles and metallic trash are also collected).
STATUS Not endangered. The status of a large island form (on Zanzibar, *C. cosensi*) is most like *C. emini* but its status requires further investigation.

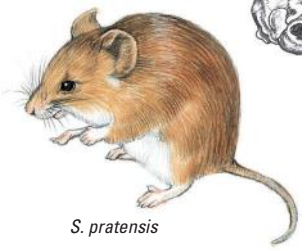
POUCHED MICE *Saccostomus*

MEASUREMENTS HB 115–190mm. T 30–80mm. W 40–85g.
RECOGNITION Grey or greyish-brown mice with short, limp fur, enormous cheek-pouches, and short legs and tail. They are strictly nocturnal.
SPECIES *S. campestris* (southern Africa), *S. mearnsi* (E Africa).
HABITAT Savannas, woodlands and semi-arid habitats in southern and East Africa. Animals use the burrows of other species as well as digging their own.
FOOD Seeds, fruits and occasionally insects.
STATUS Not endangered.

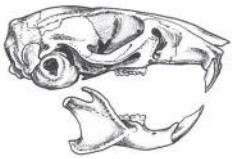


S. campestris

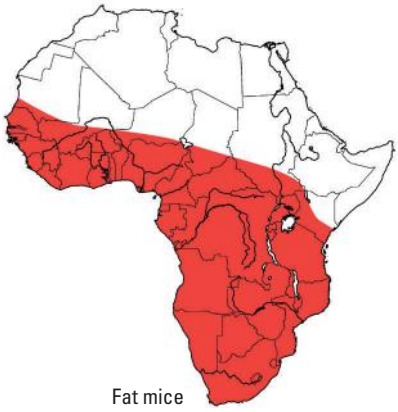




S. pratensis



S. opimus



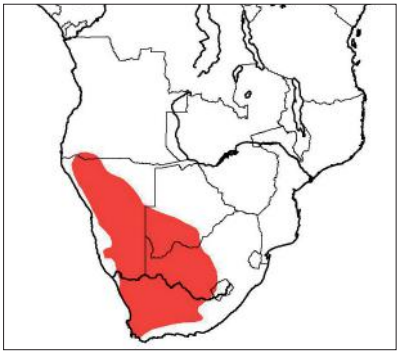
Fat mice

FAT MICE *Steatomys*

MEASUREMENTS HB 50–140mm. T 30–75mm. W (est.) 15–30g.
RECOGNITION Small mice with large ears and short limbs and tail. Upperparts are sandy-brown and underparts white. They are often very fat and lethargic.
SPECIES *S. bocagei*, *S. caurinus*, *S. cuppedius*, *S. jacksoni*, *S. krebsii*, *S. opimus*, *S. parvus*, *S. pratensis*.
HABITAT Savannas, woodlands and (marginally) semi-arid environments. Very local in distribution, fat mice are apparently absent over large intervening areas. They live in deep burrows where they store food and aestivate.
FOOD Seeds, bulbs, roots, insects, grass.
STATUS *S. jacksoni* in Ghana and W Nigeria is probably rare. All other species are widely distributed. Not endangered.

LARGE-EARED MOUSE *Malacothrix typica*

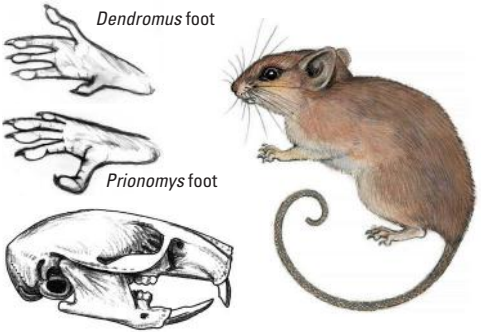
MEASUREMENTS HB 70–80mm. T 32–40mm. W 10–20g.
RECOGNITION A small, prettily marked mouse with ash-grey streaks on the back and flanks and a tawny face and shoulders. The underside and fur at the base of the very large ears are white. The tail is short and tapered. This species is nocturnal. This genus bridges the fat mice and the climbing mice inasmuch as it shares features with both taxa: genetically it is closest to the climbing mice.
HABITAT Areas of short grass and karoo bush growing on or close to calcareous pans in dry SW Africa. This mouse digs deep burrows among low bushes.
FOOD Seeds and green plant parts.
STATUS Poorly known.

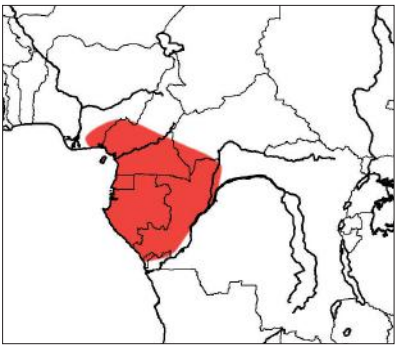


Large-eared Mouse

CLIMBING MICE
'Dendromurine' nesomyids

Climbing mice of the genus *Dendromus* are a highly specialised but successful branch of an ancient lineage. Kenyan fossils are known from 14 mya and by 8 mya they appear in Arabia and Spain (and, rather dubiously, fossils from Thailand and Pakistan have been thought to be related). Later fossils appear in various parts of Africa. Because *Dendromus* shares features with many other nesomyids the taxon 'Dendromurinae' has, over time, had very elastic and elusive boundaries.

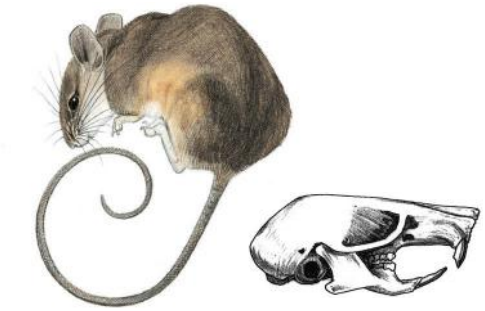


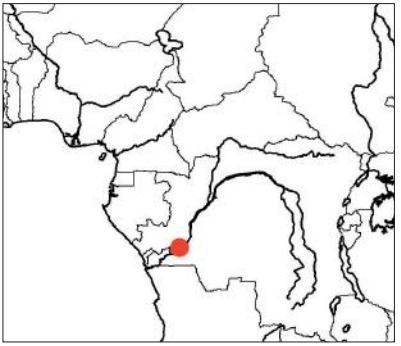


Bates's Climbing Mouse

BATES'S CLIMBING MOUSE *Prionomys batesi*

MEASUREMENTS HB 54–78mm. T 67–103mm. W (est.) 10–13g.
RECOGNITION Shrew-like, velvety fur of a deep pink-tinged tawny-brown, blending into pinkish grey underparts. Eyes are surrounded by a narrow mask of black fur. Like shrews, strongly scented. Skull specialised for ant-eating and burrowing. Instead of building arboreal nests, excavates soft soils with mole-rat-like teeth and lines end chamber with leaves. Hindfeet have well-developed opposable 'thumbs', as in primates and unlike climbing mice.
HABITAT Moist rainforest zone between Congo R. and Bight of Benin. Found in fine-stemmed shrubbery and among tangles of fine creepers.
FOOD Leaf-nesting ants and spiders.
STATUS Thought to be rare.





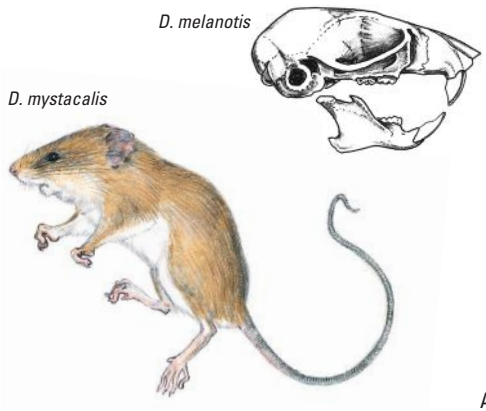
Velvet Climbing Mouse

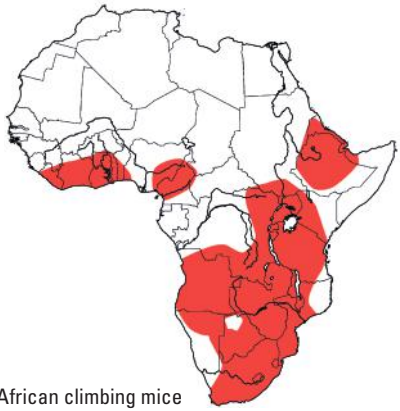
VELVET CLIMBING MOUSE *Dendroprionomys rousseloti*

MEASUREMENTS HB 77mm. T 108mm. W (est.) 10g.
RECOGNITION Very small, velvety-furred, dark-brown climbing mouse with tawny flanks and a white underside. It has a black patch of fur below the eyes and a long, prehensile tail. Because some features resemble those of Bates's Climbing Mouse (*Prionomys batesi*) it seems likely that this species also has a peculiar, but less highly specialised, niche.
HABITAT Only known from the zoological gardens on the banks of the Congo R. at Brazzaville.
FOOD Unknown but thought to include insects.
STATUS Only eight specimens known.

AFRICAN CLIMBING MICE *Dendromus*

MEASUREMENTS HB 50–100mm. T 65–110mm. W 7–23g.
RECOGNITION Large-headed climbing mice with long, semi-prehensile tails, long, extremely dextrous toes and a peculiarly specialised, 'padded hook' , four-fingered hand. Coat colour varies from pale fawn to grey or a rich brown. Undersides are usually white. Ears vary in size and shape.





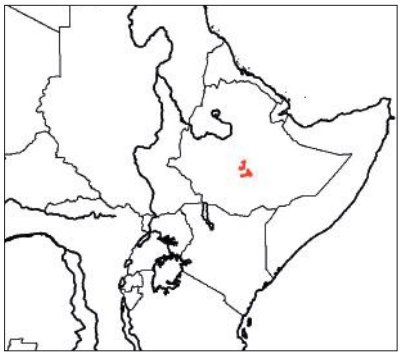
African climbing mice

SPECIES *D. insignis*, *D. kahuziensis*, *D. kivu*, *D. lovati*, *D. melanotis*, *D. mesomelas*, *D. messorius*, *D. mystacalis*, *D. nyikae*, *D. oreas*, *D. vernayi*.
HABITAT Tall grass and shrubby secondary growth, in which these mice are rapid and adept climbers. They build large, globular nests.
FOOD Specialist grass-seed-eaters.
STATUS A diverse and successful group but some species have very restricted montane distributions.

GIANT CLIMBING MOUSE

Megadendromus nicolausi

OTHER NAMES Bale Climbing Mouse, Nikolaus's African Climbing Mouse.
MEASUREMENTS HB 98–129mm. T 86–106mm. W 40–66g.
RECOGNITION A large climbing mouse with dark-brown upperparts, a black dorsal stripe and pale underside. Digits are adapted to climbing. The tail is long, fine and flexible but relatively shorter than in *Dendromus*. First described in 1978.
HABITAT High altitudes in the Bale massif in central Ethiopia. It has been caught in everlasting sage-brush (*Helichrysum*- and *Artemesia*-dominant) and among mountain grasses (*Andropogon*, *Festuca* and *Poa*).
FOOD Probably grass seed.
STATUS Extremely localised in a zone threatened by settlement and ever more intensive grazing by sheep and goats. Vulnerable or endangered.



Giant Climbing Mouse

CRICETID MUROIDS CRICETIDAE

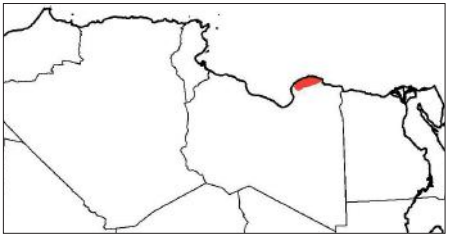
True cricetids are a New World and Holarctic group of rodents with relatively conservative molar teeth, and today are almost entirely absent from Africa. In this work only one species, the very marginal Mediterranean Vole *Microtus guentheri*, is treated as a cricetid. However, until quite recently many African rodents were, rather uncertainly, allocated to Cricetidae. Molecular science has confirmed the need for caution, indicating that the Crested Rat *Lophiomys* is the single survivor of an extremely ancient lineage, deriving from near, but essentially *after* the point where ancestral cricetids and murids diverged in the Miocene.

Previous allocations of *Lophiomys* to one or the other lineage largely depended upon which morphological features were chosen. Tooth structure, for example, firmly places *Lophiomys* in Cricetidae. On the other hand, genetics suggest a closer affinity with the *Deomyinae* and *Gerbillinae*, which have also occupied an ambiguous genetic position in between cricetids and murids. In this guide, crested rats (Lophiomyinae), the hair-modified rats (Deomyinae) and gerbils (Gerbillinae) are treated as genetic murids but their claims as dental cricetids still deserve recognition.

Voles (Arvicolinae) are adapted to low temperatures, mainly ranging through cool or cold Holarctic environments where there are many species and genera. The sole African species would appear to be a relict from a period close to a glacial maximum, possibly the most recent peak about 20,000 years ago. Not only is it likely to be a very recent immigrant, but as a *Microtus* vole it belongs to a very recently evolved type of temperate and cold-adapted rodent.

MEDITERRANEAN VOLE

Microtus guentheri



Mediterranean Vole

MEASUREMENTS HB 109–125mm. T 20–25mm. W 25–40g.

RECOGNITION A short-tailed, blunt-eared, tubby, brown rodent with very distinctive molar teeth. Molars grow continuously, with crenellated enamel surfaces with cement infill in a mill-like structure that can support side-to-side mastication of abrasive silicaceous grasses.

HABITAT Voles are cold/temperate animals and this species undoubtedly colonised the Mediterranean *Macchia* vegetation of Cyrenaica during quite recent Glacial times. Today, the heights of the Cyrenaic plateau help generate the lower temperatures that favour the survival of this rodent. Voles congregate in colonial burrows that are shallower in humid soils (5–10cm deep), deeper (up to a metre) in drier soils. They have a well-developed vocal repertoire.

FOOD Roots, seeds and leaves: taken down into burrow to eat.

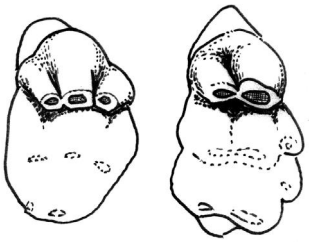
STATUS Rapid breeders, with 3 weeks' gestation and up to 12 young.

MURIDS MURIDAE

Crested (Maned) Rat	Lophiomyinae (1 species)
Hair-modified rats	Deomyinae (30 species)
Togo Mouse	Leimacomyinae (1 species)
Gerbils	Gerbillinae (71 species)
Rats and mice	Murinae (156 species)

Rats and mice are so alike that, over the years, ideas about their relationships became deeply layered and ever more confusing. Now a more objective muroid phylogenetic tree has begun to emerge, thanks to new genetic methods. Even so, decisions as to where to draw lines between taxa can still be a matter of choice. This remains true for the cricetid/murid divide.

When teeth provided the primary (often only) basis for classification, gerbils and various rats with double-cusped molars were quite logically classed as cricetids. Genetic analysis has now revealed that the hair-modified rats (Deomyinae), like gerbils and the Crested Rat, derive from close to, but just *after* the period in which cricetids and murids had differentiated. Unlike the first edition of this guide, when such molecular analyses had not begun, these taxa now fall on the murid side of the divide.



Murid (*left*) and cricetid (*right*) molars.

Nonetheless the three major groupings that follow are no less different from all other murines than they were before. If anything, their many peculiarities invite even more attention, manifesting, as they do, many ingenious rodent adaptations to living on a continent of extraordinary and challenging complexity.

Because murid rodent subgroups are now easier to separate genetically, my once undifferentiated catalogue of rats and mice has been broken down into a series of identifiable mini-radiations. These broadly correspond with the latest published molecular trees.

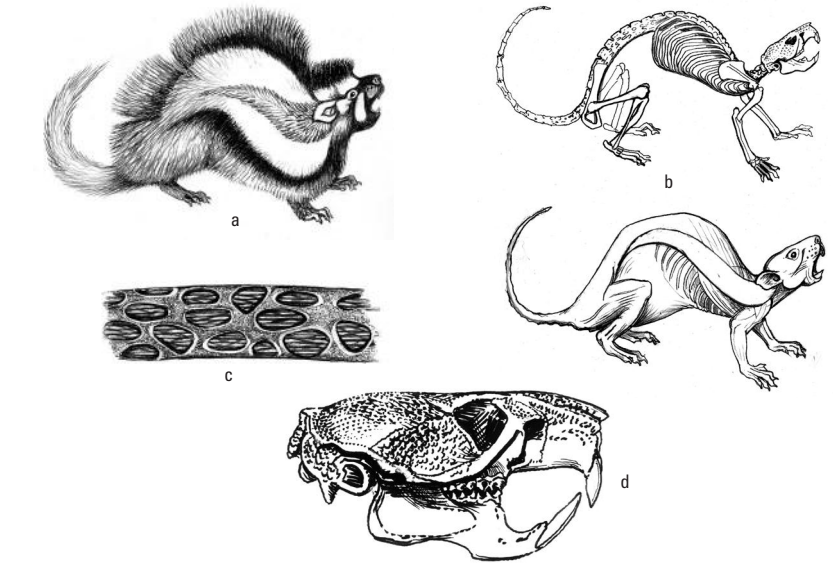
While the murid radiation remains poorly understood, it still embraces a great diversity of groups, including omnivorous, herbivorous and yet further specialist offshoots.

CRESTED (MANED) RAT Lophiomyinae

This singular rodent is one of the most interesting and extraordinary of African mammals. Its isolated position among rodent taxa and a wide scatter of likely 'lophiomyine' fossils from the Miocene implies that this rodent's specialisations have very deep evolutionary roots. Interpretations of its affinities, morphology and behaviour are mostly very recent and learning that it is deadly poisonous has earned the Crested Rat a special claim to fame. Its poison is sequestered in a long, tapered tract of specialised hair running back from behind the ear across the flanks to the groin. It shares the peculiarity of specialised hairs with spiny mice and other hair-modified rats, deomines, its relatives (albeit rather distant). This hair tract is normally hidden beneath long grey fur but it is one of several unique features, every one implying anticipation, defence or resistance to attack.

For a start, its skin is exceptionally dense, thick and resistant to being pierced. Likewise, its skull is roofed over with granulated bone to form a cranial helmet that resembles that of a turtle. Near-atrophy of the clavicles has effectively freed up the broad scapulae to shield the neck and thorax when the shoulders are hunched. Like a pair of turtle scutes, these 'floating shoulder-blades' are made all the more mobile by particularly well-developed attachment muscles. Vertebrae have enlarged and multiplied, their spines have shortened, which has made the entire vertebral column (especially the neck) unusually robust and flexible compared to those of other rats.

The tract of poisoned hairs is exposed by means of specially modified dermal muscles that erect the long, externally grey fur upwards above it and deflect it downwards below the poison tract. Flaring of the fur, triggered by any external interference or attack on the animal, reveals bold white-and-black bands on either side of the spongy hair tract. The effect is somewhat skunk- or



Crested Rat: (a) External warning (aposomatic) pattern in defensive posture. Display serves to expose a specialised hair tract and focus attention on neck and shoulder. (b) *Above:* Skeleton showing damage-mitigating features of skull and skeleton: cranial 'helmet', 'floating' scapulae and robust vertebrae. *Below:* Schematic myology showing position of area underlying specialised hair-tract. (c) Vacuolated hair-shaft enclosing numerous fine filaments that 'wick' secretion. (d) Reinforced, 'helmeted' skull. The molecular and physiological details of this mammal's toxin-management systems have significant future implications for human health, making it potentially one of the most important and interesting rodents in Africa.

zorilla-like. The animal pulls its head back into its shoulders, hisses and turns its flared, haloed tract towards its adversary, as if actively inviting a bite!

The main shaft of each specialised hair has a thin but strong outer cylinder perforated by abundant vacuoles. This outer lattice encloses abundant long fine fibres that act as a 'wick' that absorbs and holds secretions that can travel by capillary action along the interior of each hair cylinder. Once a hair has become saturated the secretion then becomes semi-viscous or waxy but the hairs' open lattice-work ensures that the hairs cannot be touched without direct contact with the secretion. What is this deadly secretion and how do the hairs soak it up?

The answer involves an astonishing association between this rat and very toxic plants belonging to the Apocynaceae, most notably the celebrated 'poison-arrow trees' *Acokanthera* spp. which secrete a cardiac glucocide, ouabain, in their bark and roots. *Lophiomys* seek out the tree, then chew up and carefully slaver a colloid of 'poison arrow' poison and saliva onto the flank hairs, which rapidly wick up the colloid.

With a long evolutionary history of herbivory, *Lophiomys* ancestors would have enjoyed a natural tolerance for plant toxins in general. Natural selection has refined this intrinsic rodent advantage, step by step, to the point where modern *Lophiomys* can masticate *Acokanthera* bark or roots without ill effect. Lacking any exposure to plant toxins in their history, carnivores are particularly susceptible to ouabain. When dogs bite *Lophiomys* they exhibit symptoms of extreme distress, sometimes foaming at the mouth almost instantaneously. In some cases poisoned dogs die with startling rapidity, apparently from heart failure. Local naturalists have reported finding cadavers of wild carnivores supposedly poisoned in similar fashion. There are abundant instances of insects (and some birds) using plant toxins to deter or poison their predators but this is the first instance of something comparable taking place among mammals.

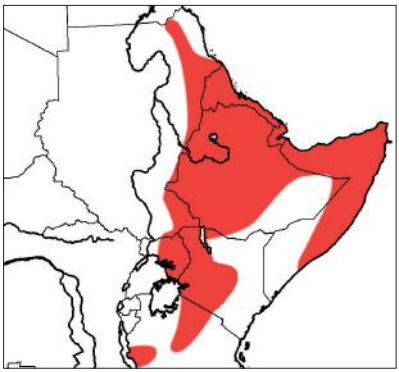
Fossils allocated to Lophiomyinae have been found in Miocene Africa and Europe and *Lophiomys* is also known from more recent archaeological sites in the Middle East, but today the single living genus/species is confined to north-eastern Africa.

CRESTED (MANED) RAT

Lophiomys imhausi

MEASUREMENTS HB 180–360mm. T 140–215mm. W 590–920g.

RECOGNITION A normally inconspicuous, slow-moving, mainly nocturnal rodent with dense, woolly grey fur and black-and-white markings on the face. Muzzle and feet are the only areas of short fur. Long bicoloured hairs above and below the flanks are able to part to reveal a tract of hairs that resemble hemp string in texture and colour. As detailed above, these are among the most highly modified hairs of any mammal. The stomach has become weakly sacculated but the configuration is far short of the compartments of a typical ruminant. Nonetheless a complex digestive system is implied and both the processing of plant nutrients and neutralising of toxins are probably involved. Large salivary glands also suggest adaptation to metabolise plant toxins. Digestive fermentation in the large intestine and caecum is the norm in murids.



Crested Rat

The possible presence and activity of symbiotic microflora and microfauna in the foregut of Crested Rats would therefore be of special interest and invites research. The Crested Rat is a skilful, but slow climber and uses its hands like a squirrel to manipulate foods while squatting on its haunches.

HABITAT Mostly steep, rocky valleys within woodlands and montane forests under variable, but typically seasonal, rainfall. Especially noted from juniper forests with abundant poison-arrow trees, *Acocanthera* spp. Ranges from sea level to over 3,000m. Sometimes shares its habitat with rock hyraxes.

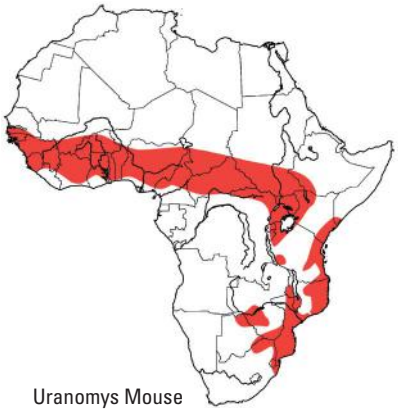
FOOD Mainly shoots and leaves for which its elaborate digestive system may be specially adapted.

STATUS Seldom seen, possibly common in isolated pockets of suitable habitat but otherwise certainly in decline overall. Its survival is predicated upon *Acokanthera* trees continuing to be abundant.

HAIR-MODIFIED RATS Deomyinae

Uranomys Mouse	*Uranomys ruddi*
Link Rat	*Deomys ferugineus*
Brush-furred mice	*Lophuromys* (15 species)
Spiny mice	*Acomys* (13 species)

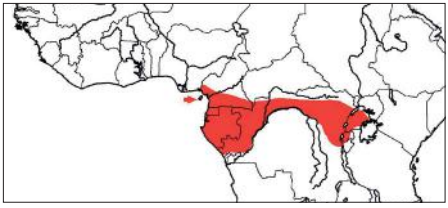
URANOMYS MOUSE *Uranomys ruddi*



Uranomys Mouse

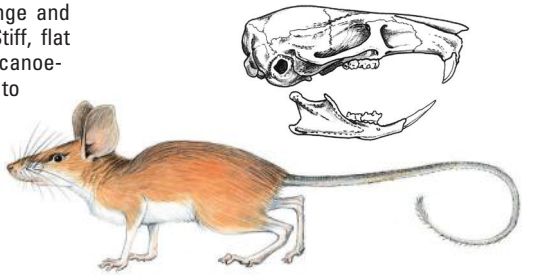
OTHER NAMES Rudd's Brush-furred Mouse.
MEASUREMENTS HB 101–119mm. T 55–68mm. W 31–51g.
RECOGNITION Chunky, semi-fossorial mouse with skull somewhat reminiscent of a miniature mole-rat, short, rounded ears, both fore- and hindlegs very short, coarse, brush-textured coat. Coloration is very variable, ranging from near black to pale grey, fawn or russet. Underparts white.
HABITAT Tropical species showing a preference for *Hyparrhenia* grassland with Borassus Palms (*Palmyra borassus*) growing in generally friable soils. Disconnected records from Senegal to Uganda to Malawi.
FOOD Omnivorous, including ant pupae and bulbs, probably foraged from underground. Little known, but likely to be a useful indicator species for quite precise soil conditions and subterranean ecology.
STATUS Very wide but scattered distribution; status little known.

LINK RAT *Deomys ferugineus*

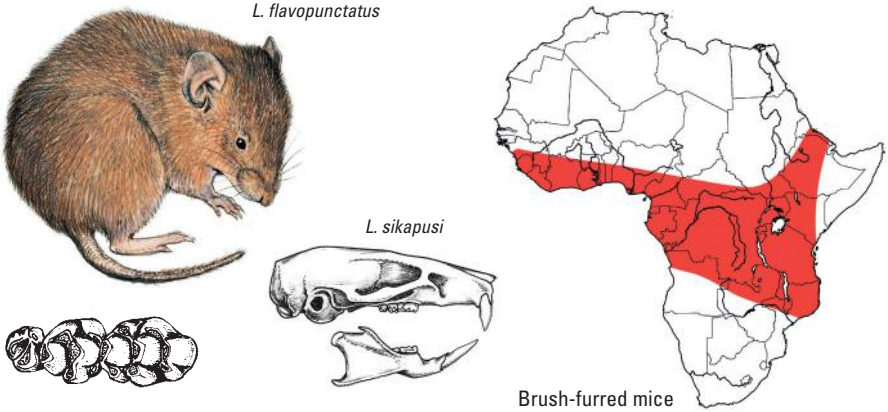


Link Rat

OTHER NAMES Rusty Link Rat, Congo Forest Rat.
MEASUREMENTS HB 115–150mm. T 159–202mm. W 40–77g.
RECOGNITION The Link Rat is highly distinctive for its long legs, pointed, narrow head surmounted by enormous ears, and strong scent. It has a very long, bicoloured tail. The back and forehead are rich orange and brown and the underside is white. Stiff, flat rump and dorsal hairs have unique 'canoe-like' cross section, well-suited to retaining (unknown) secretions or substances. It can be conjectured that the peculiar structure of the hairs is somehow connected with the deterrence of predators. It is nocturnal and crepuscular.



HABITAT In dry season prefers flooded forest floors: in wet season, less constrained. This strictly equatorial species ranges north of the Congo R. from Mt Cameroon to the Victoria Nile.
FOOD Mainly insects, crustaceans, slugs and some fallen fruits (notably palm-nut husks).
STATUS Widespread but scattered distribution. Seldom very common.

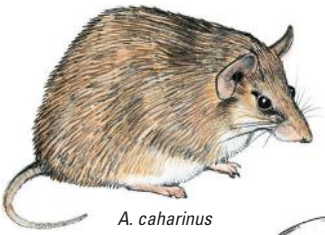


BRUSH-FURRED MICE *Lophuromys*

MEASUREMENTS HB 89–180mm. T 30–100mm. W 28–142g.
RECOGNITION Compact African mice with short legs and tails. The dark or speckled coats have a brush-like texture, probably designed to dispense obnoxious, deterrent secretions. These mice are omnivorous surface foragers, like shrews, and, like shrews, are strongly scented (possibly on a gradient of distastefulness). There are diurnal and nocturnal lineages. The most conservative (*woosnami*) group (*L. woosnami*, *L. luteogaster*, *L. medicaudatus*) are relict species restricted to patchy highland habitats in central Africa. A second (*sikapusi*) group are long-clawed, nocturnal, sometimes sub-surface foragers with a strong preference for very moist, mainly forested, habitats. *L. sikapusi* has a coast-to-coast tropical African distribution. The very closely related *L. nudicauda* and *L. huttereri* have patchy centre–west distributions, while *L. roseveari* survives only on uppermost Mt. Cameroon. The remaining species, mainly diurnal, surface foragers of the *L. flavopunctatus* group, have three highland centres of endemism. One is in Cameroon highlands (*L. eisentrauti* and *L. dieterleni*), another in Ethiopia (*L. brevicauda*, *L. chrysopus* and *L. melanonyx*) and another in central Africa (*L. cinereus*, *L. rahmi*). *L. flavopunctatus* is by far the most successful, widespread and adaptable of all the brush-furred species (possibly assisted by a notably repulsive scent).
SPECIES *L. brevicaudus*, *L. chrysopus*, *L. cinereus*, *L. dieterleni*, *L. eisentrauti*, *L. flavopunctatus*, *L. huttereri*, *L. luteogaster*, *L. medicaudatus*, *L. melanonyx*, *L. nudicaudus*, *L. rahmi*, *L. roseveari*, *L. sikapusi*, *L. woosnami*.
HABITAT Moist, grassy areas of tropical Africa from sea level to about 3,000m.
FOOD Invertebrates, especially ants, carrion and plant material.
STATUS Overall a very successful group, but some species occupy tiny ranges in localities that are desirable for agriculture.

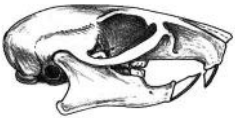
SPINY MICE *Acomys*

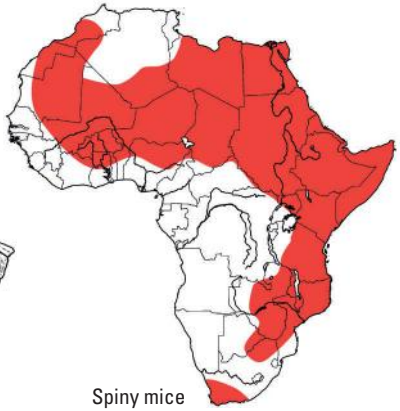
MEASUREMENTS HB 70–120mm. T 40–100mm. W 10–40g.
RECOGNITION Mice with short limbs and tail and very spiny, coarse fur. Like porcupines, their spines are shed easily and thin skin is easily torn. Upperparts are rufous or fawn to grey or brown and underparts are white or tinted.
SPECIES A small hair-modified ancestor probably first emerged during a dry period of the Miocene along the arid corridor that linked eastern and southern Africa. Genetically conservative remnants of this primary adaptive phase are represented by *A. subspinosus* in the Cape, *A. subspinosissimus* in south-eastern Africa and *A. percivali* in some Precambrian granitic and Rift Valley habitats in eastern Africa (*A. wilsoni* could represent a slightly later derivative of *A. percivali type*). Genetically



A. caharinus

A. caharinus





Spiny mice

these early forms of African spiny mice include a small diurnal species, *A. russatus*, which ranges from the Nile delta down the length of western Arabia, implying an early spread out of Africa. With progressive adaptation to drought, heat and rocky environments a second phase emerged. *A. louisae*, *A. mullah*, *A. kempi*, *A. ignitus*, *A. johannis* and *A. cineraceus* represent a tentative grouping of the secondary *Acomys* radiation. The third radiation probably began with an ancestral population of *A. dimidiatus* in Asia, an exceptionally adaptable and nocturnal species, often regarded as synonymous with *A. caharinus*. The latter is a true desert species, occupying all the northern reaches of the Sahara desert and Red Sea littoral. A sibling species, *A. airensis*, inhabits the south-western Sahara.

HABITAT Deserts and dry areas from the Mediterranean to the Cape. Absent from all humid zones and from the Namib and Kalahari, a region that should suit them. Prior occupation of the south-west by rodents with parallel adaptations (*Petromus*, *Petromyscus*, *Malacothrix*) presumably pre-empted *Acomys*. Spiny mice are dependent on natural shelter in minute crevices in or beneath rocks, in gerbil or other rodent warrens, in termitaries, tree trunks or houses.

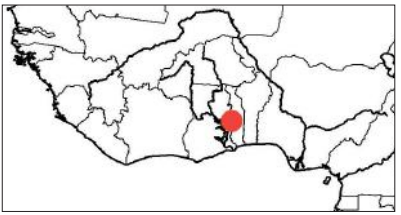
FOOD Opportunistic but preferences vary by species; invertebrates, seeds, leaves, dry plant matter.

STATUS Considered a pest in some dry settlements, where it may come into houses. Not endangered.

TOGO MOUSE Leimacomyinae

An entire subfamily, genus and species built upon two specimens of a small mouse collected at Bismarckburg (Yege) in 1890 during the colonisation of Togo. The Togo Mouse resembles a very delicate *Uranomys* in its pro-odont incisors but the molars differ.

TOGO MOUSE *Leimacomys buettneri*



Togo Mouse

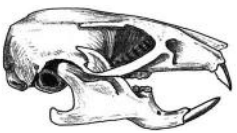
MEASUREMENTS HB 118mm. T 37mm. W (est.) 50–60g.

RECOGNITION A medium-sized brown mouse with a very short, tapered tail and paler fawn flanks and shoulders. It has small, well-haired ears and well-developed claws on the forefeet. Teeth are grooved.

HABITAT Not known but collected within the 'Dahomey Gap', a savanna–forest–mosaic region separating the Upper Guinea and Nigerian forests.

FOOD Delicate, pincer-like teeth and muzzle suggest small, soft-bodied insects or unripe seeds may be main foods.

STATUS Possibly extinct. Extremely localised and little known.



GERBILS Gerbillinae

Fat-tailed Gerbil	*Pachyuromys duprasi*
Brauer's Dwarf Gerbil	*Desmodilliscus braueri*
Namaqua Gerbil	*Desmodillus auricularis*
Slender gerbils (Taterils)	*Taterillus* (8 species)
Sand rats	*Psammomys* (2 species)
Jirds	*Meriones* (3 species)
Bushy-tailed Jird	*Sekeetamys calurus*
Gerbils	*Gerbillus* (36 species)
Peel's Pygmy Gerbil	*Microdillus peeli*
Walo (Ammodile)	*Ammodillus imbellis*
Robust gerbils	*Gerbilliscus* (syn. *Tatera*) (12 species)
Hairy-footed gerbils	*Gerbillurus* (4 species)

Nocturnal desert rodents with well-muscled and longer hindlegs and more slender forelegs. They are mostly of sandy colouring and have large eyes and enlarged inner ears. External ears vary in size and shape.

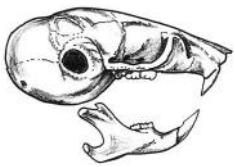
Gerbils are probably of Eurasian origin and have only been recorded as fossils in Africa from about 7 mya. Older genera are essentially Eurasian immigrants. Others have evolved more recently in Africa. Most genera are restricted to arid areas of Africa but several types have adapted to sandy soils or semi-arid zones within the tropics.

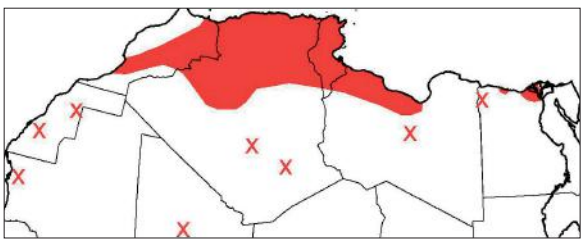
Their ecological success has been greatly assisted by drought-resistant physiology, the digging of extensive burrows and the storing of food. Secure burrows have allowed gerbils to raise litters of blind, naked young that develop relatively slowly. Principal foods are seeds and vegetable matter but many species eat invertebrates.

Food storage probably originated as a response to Eurasian winters. Social living contributes to collection of food, strengthens defences against other rodents and helps to reduce heat loss during winters. Food-rich corners of the desert can support social gerbils of Asian origin (i.e. *Meriones* and *Psammomys*) while poorer areas sustain solitary gerbil types.

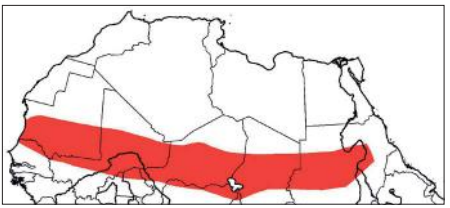
FAT-TAILED GERBIL *Pachyuromys duprasi*

OTHER NAMES Fat-tailed Jird.
MEASUREMENTS HB 105–135mm. T 45–61mm. W 30–65g.
RECOGNITION A small gerbil with a pale, soft coat, pinkish-buff sides and white underparts. The short, fat-covered tail is almost naked and the forefeet are well clawed. Incisors are faintly grooved. Inner ear bullae are vastly inflated.
HABITAT Deserts in N Africa with solid substrates. Populations are thought to fluctuate.
FOOD Omnivorous, includes fruits, gathered as far as 2km from the burrows in which they are stored.
STATUS Little known.





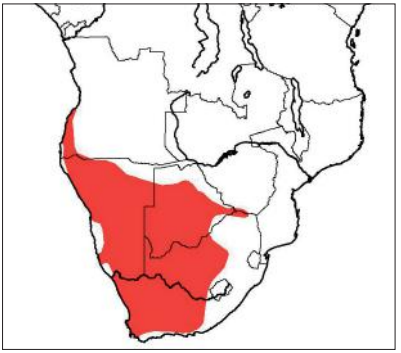
Fat-tailed Gerbil



Brauer's Dwarf Gerbil

BRAUER'S DWARF GERBIL *Desmodilliscus braueri*

OTHER NAMES Pouched Gerbil.
MEASUREMENTS HB 50–70mm. T 35–50mm. W (est.) 8–15g.
RECOGNITION A very small, soft-furred, fawn gerbil with white spots behind the ears, small hindfeet, and a tail shorter than the body. It has large cheek pouches. The inner ear bullae are very large. Only two molars. Thought to be social.
HABITAT Sahelian steppes on sandy or gravelly soils from Mauritania to Sudan, vicinity of Khartoum. Digs short, shallow burrows with numerous exits/entrances.
FOOD Presumed to be grass seeds, stored in burrows.
STATUS Widely distributed but little known.



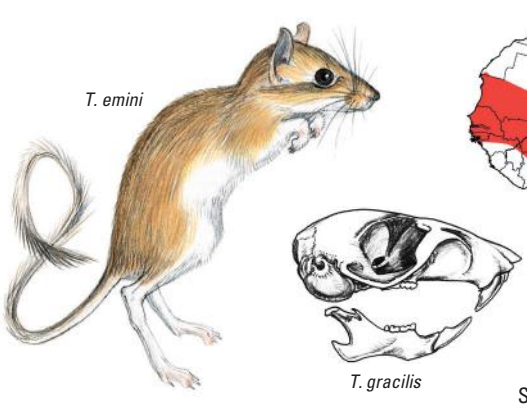
Namaqua Gerbil

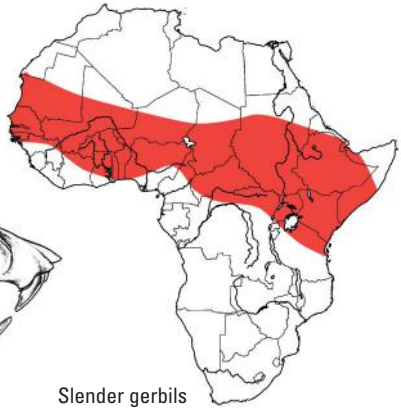
NAMAQUA GERBIL *Desmodillus auricularis*

OTHER NAMES Cape Short-tailed Gerbil.
MEASUREMENTS HB 100–140mm. T 80–100mm. W 39–70g.
RECOGNITION Large-eyed, variably coloured gerbil with short hindlegs. The tail is shorter than the body and there is white fur behind the flesh-coloured ears. The inner ear bullae are vastly inflated.
HABITAT SW Africa, Kalahari, Karoo and Namibian deserts, where this gerbil is associated with open pans and compacted calcareous soils. The burrows of this species are unusual for their almost vertical exit holes.
FOOD Omnivorous with seasonal switches from seeds of grasses in winter, insects and green material in summer. Stores in burrows.
STATUS Not endangered.

SLENDER GERBILS (TATERILS) *Taterillus*

MEASUREMENTS HB 100–140mm. T 140–170mm. W (est.) 50–80g.
RECOGNITION Smaller tawny gerbils with white bellies, long, hairy tails and long jumping hindlegs. Eyes large but internal ear bullae relatively smaller than in most gerbils. The genetics of this genus are complex and the status and naming of species is a work in progress.





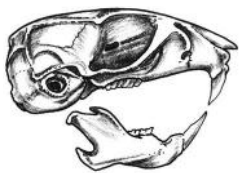
Slender gerbils

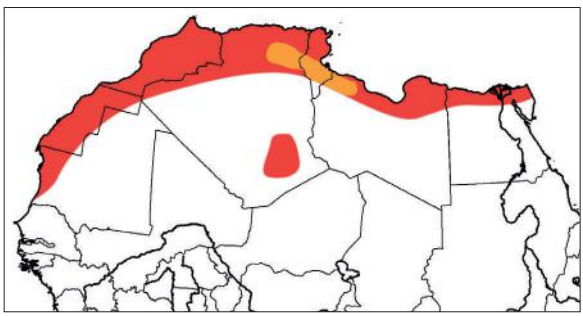
SPECIES *T. arenarius*, *T. congicus*, *T. emini*, *T. gracilis*, *T. lacustris*, *T. petteri*, *T. pygargus*, *T. tranieri*.
HABITAT Mainly Sudanic and Sahelian savannas and steppes along the southern borders of the Sahara. Digs burrows.
FOOD Nocturnal foragers for various plant foods and insects, the latter mainly in the dry season.
STATUS Diverse species in widely scattered, often Saharan, habitats where life histories are unknown.

SAND RATS *Psammomys*

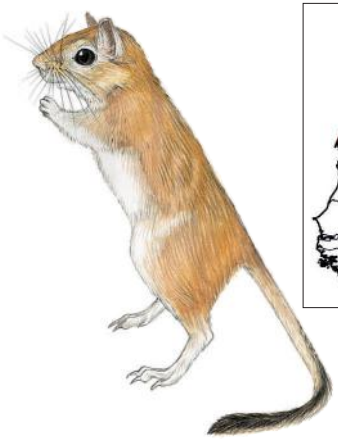
MEASUREMENTS HB 130–180mm. T 110–150mm. W (est.) 50–75g.
RECOGNITION Unusually for gerbils, these species are diurnal. They are relatively large with long buffy fur, with numerous long, fine guard hairs. Ears are thick, short and oval.
SPECIES *P. obesus* (common and widespread), *P. vexillaris* (rare, centred in regions close to Tunisia).
HABITAT Live in extensive burrows, excavated among the roots of shrubs and bushes growing on firm, compacted sands in valleys and on alluvial plains, salt-brush floodplains and neighbouring slopes in the Sahara Desert from Morocco to Egypt.
FOOD Highly specialised to feed on the leaves and stems of salty succulents, notably *Suaeda*, *Traganum* and *Salsola*, eaten in large quantities with frequent excretion of very salty urine (deposits of which are characteristic of their burrow entrances).
STATUS Very common in appropriate halophytic steppes.

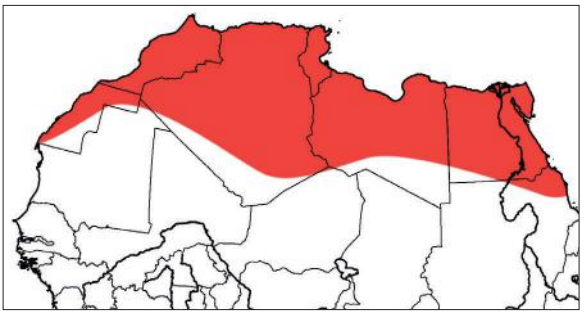
P. obesus



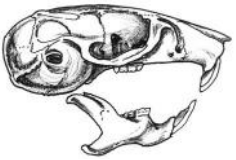


Sand rats





Jirds



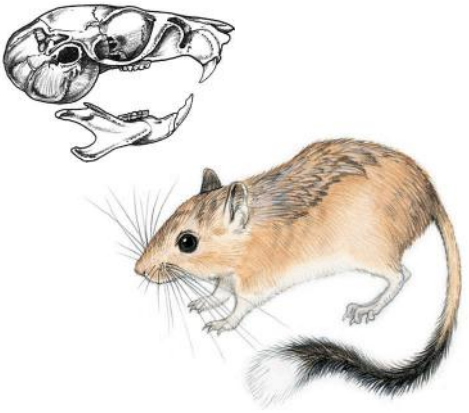
M. libycus

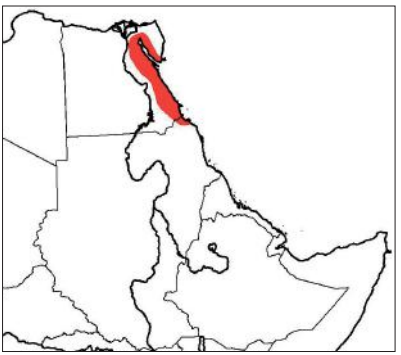
JIRDS *Meriones*

MEASUREMENTS HB 110–130mm. T 90–110mm. W (est.) 50–75g.
RECOGNITION Sandy-coloured, robustly built gerbils with relatively short, narrow feet and a tufted, dark-tipped tail. They are capable of climbing trees and rocks. Social behaviour is flexible (social in some areas, solitary in others). They build complex burrows.
HABITAT Various desertic and subdesertic habitats in N Africa, Niger, Chad and Sudan.
SPECIES *M. crassus*, *M. libycus*, *M. shawi*.
FOOD Seeds, stems, leaves, roots and bulbs (often stored in burrows).
STATUS Not endangered.

BUSHY-TAILED JIRD *Sekeetamys calurus*

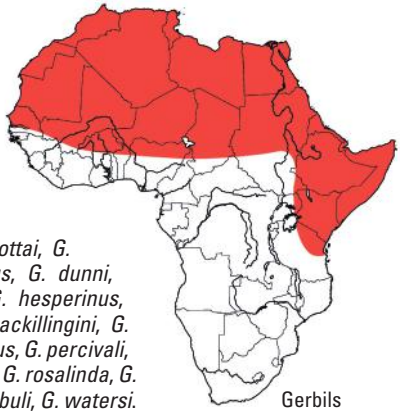
MEASUREMENTS HB 100–125mm. T 110–160mm. W (est.) 30–60g.
RECOGNITION An agile, rock-dwelling gerbil with dense, soft fur. Mantle of brownish streaking over pale sandy-coloured sides; white belly. Tail long and brown or black towards the end, with bushy white tip, carried squirrel-fashion, arched over back.
HABITAT Broken rocky country in Egypt, where it burrows under rocks and slabs, often in hilly country or on slopes. It is an agile climber and jumper.
FOOD Nocturnal forager for arthropods, seeds and leaves.
STATUS Thought to be relatively long-lived but biology little known.





Bushy-tailed Jird

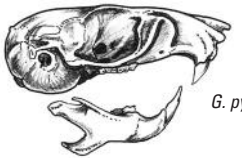
GERBILS *Gerbillus*



Gerbils

MEASUREMENTS HB 70–120mm. T 80–150mm. W 15–25g.
RECOGNITION Small gerbils with very long hindlegs and short front legs. Soles of the feet are naked in some species, hairy in others. Most have white fur above the eyes or behind the ears. The majority of species are Saharan and the genus requires a comprehensive molecular review. Many species are gregarious. (The inner ear bullae are very large.)
SPECIES *G. acticola, G. amoenus, G. andersoni, G. bottai, G. brockmani, G. campestris, G. cosensis, G. dasyurus, G. dunni, G. floweri, G. gerbillus, G. harwoodi, G. henleyi, G. hesperinus, G. hoogstraali, G. juliani, G. latastei, G. lowei, G. mackillingini, G. maghrebi, G. nancillus, G. nanus, G. nigeriae, G. occiduus, G. percivali, G. perpallidus, G. pulvinatus, G. pusillus, G. pyramidum, G. rosalinda, G. rupicola, G. simoni, G. somalicus, G. stigmonyx, G. tarabuli, G. watersi.*
HABITAT Open dry and sandy habitats in N and NE Africa.
FOOD Grass, roots, seeds and insects.
STATUS Largely unknown.

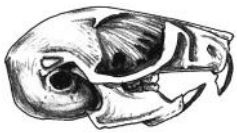
G. gerbillus

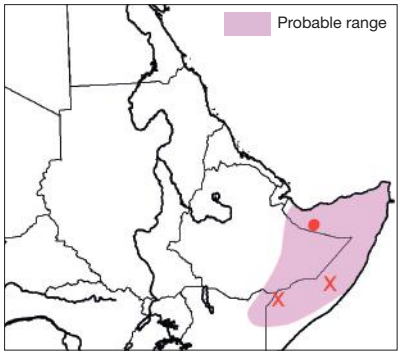


G. pyramidum

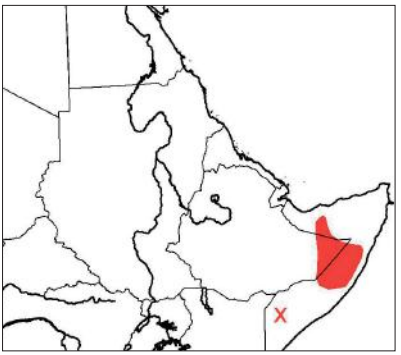
PEEL'S PYGMY GERBIL *Microdillus peeli*

OTHER NAMES Somali Pygmy Gerbil.
MEASUREMENTS HB 66–88mm. T 50–65mm. W (est.) 10–20g.
RECOGNITION Minute gerbil with fawn upperparts, extensively white below, very large eyes (for strictly nocturnal existence), sometimes fat-swollen, short tail. (Included in *Gerbillus* in previous publications.) One still-warm and perfect specimen encountered lying on a path appeared to have been abandoned immediately after its death. Since the only sign of trauma surrounded the mouth and nose, it is possible that a snake had fled immediately after emerging from the gerbil's burrow (holding it by the muzzle).
HABITAT Somali desertic, mostly sandy habitats.
FOOD Probably grass seeds and other vegetable matter.
STATUS Rarely seen, little known.





Peel's Pygmy Gerbil



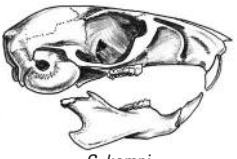
Walo

WALO (AMMODILE) *Ammodillus imbellis*

MEASUREMENTS HB 105–110mm. T (est.) 130–150mm. W (est.) 40–60g.
RECOGNITION A reddish-fawn gerbil with a long, hairy tail. The base of the ears and brows to the large eyes are white. The bare pads of the feet have an unusual granular texture.
HABITAT Recorded from sandy desert in Somalia.
FOOD The very feeble jaw structure suggests that only soft foods are taken, possibly fruits and soft-bodied insects.
STATUS Not known.

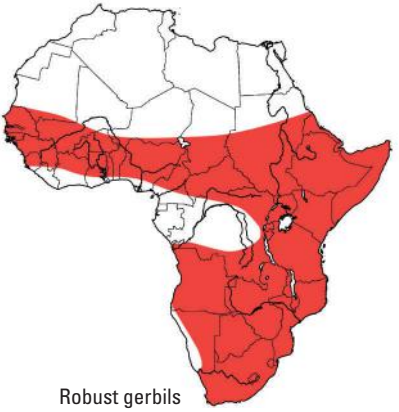
ROBUST GERBILS *Gerbilliscus* (formerly *Tatera*)

MEASUREMENTS HB 120–160mm. T 140–170mm. W (est.) 60–125g.
RECOGNITION The African branch of a primarily Asiatic group of variously coloured gerbils with long hindlegs, naked-soled feet, large eyes and ears, and a prominent, hairy muzzle. The upper incisors are grooved. Formerly included in the Indian genus *Tatera*, African species represent a secondary and little understood radiation which appears to have divided into roughly northern and southern clusters but with substantial overlaps. They commonly build extensive warrens.
SPECIES Northern sub-Saharan species: *G. gambianus, G. guinea*, *G. kempi, G. nigricaudus*, *G. philipsi*, *G. robustus*. Southern species: *G. afra*, *G. brantsii*, *G. inclusus*, *G. leucogaster*, *G. validus*. Great Lakes region and Zambezian plateau: *G. boehmi.*
HABITAT Most of sub-Saharan Africa (except rainforest areas). These gerbils inhabit well-drained, sandy areas.
FOOD Seeds, stems and roots of grasses; also roots, bulbs and insects.
STATUS A successful, diverse group.



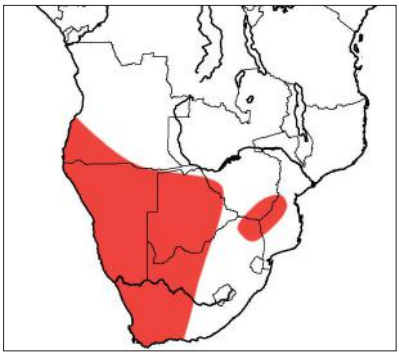
G. kempi

G. leucogaster



Robust gerbils

G. vallinus



Hairy-footed gerbils

HAIRY-FOOTED GERBILS *Gerbillurus*

MEASUREMENTS HB 80–120mm. T 100–130mm. W 22–40g.
RECOGNITION Small, pale-coloured gerbils with long tails and large, hairy hindfeet. This taxon is essentially a localised south-western radiation within the robust gerbil radiation which embraces *Gerbilliscus*, *Desmodillus* and the Indian genus *Tatera*.
SPECIES *G. paeba*, *G. setzeri*, *G. tytonis*, *G. vallinus*.
HABITAT Arid areas of SW Africa, with a preference for sandy soils. Hairy-footed gerbils excavate warrens, where they live in small groups.
FOOD Seeds and probably insects.
STATUS Little known.

RATS AND MICE Murinae

A single, subtle dental structure has long been the principal diagnostic detail for murines and is still used and useful. It consists of three separate cusps ranged across the front of the first upper molar (see illustration p.268). Murine rats and mice range from 2g to 170g in weight and may have long or short tails, limbs, noses and ears. They can have either fine and short or long and shaggy fur. Some species are patterned, others are dark or plain.

Their radiation is now better understood as genetic studies have revealed three subdivisions of the more than 30 genera and about 150 species. Two are effectively intra-African radiations, one of broadly omnivorous rats and the other of predominantly herbivorous or plant-eating species, each likely to be descended from a still uncertain number of immigrant ancestors. A third category embraces another mainly African, but later radiation of a single genus, *Mus*, and a handful of species that are all much more recent arrivals from Eurasia.

Both fossil and genetic studies agree that murines are all relatively late arrivals in Africa (the earliest about 10.5 mya). As highly fecund and active rodents, they are in the process of replacing earlier types of rodent and are the most likely reason for older, more conservative forms becoming ever more specialised or relegated to relict status.

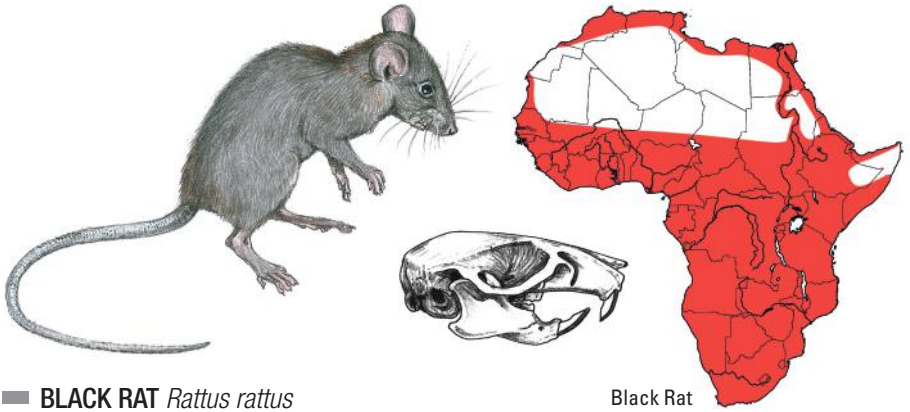
Omnivorous types ('omni-murines') are rat- or mouse-like, with a soft, short coat and irregularly cusped cheek-teeth, while herbivores ('herbi-murines') tend to be shaggier, with a blunter, vole-like head and more mill-like cheek-teeth. Some genera form closely related clusters, which may be associated with particular ecological and geographic regions. The more specialised species are so well adapted to local peculiarities of particular ecosystems that they can be very abundant in just one locality or ecotype and nowhere else. Regional ecosystems began with fewer murine rodent lineages and what we see today is an ongoing drama of rodent contention in which the particular suite of species is constantly changing, usually in favour of the more recently evolved. Biogeographic regions are sometimes associated with particular rodent groups, thus both omni-murine and herbi-murine suites are found in the East African and Ethiopian uplands and equivalent radiations have occurred in the rainforests of equatorial central Africa.

RECENT IMMIGRANT MURINES AND DESCENDENTS

Black Rat	*Rattus rattus*
Short-tailed Bandicoot Rat	*Nesokia indica*
Long-tailed Field Mouse	*Apodemus sylvaticus*
Common mice	*Mus* (20 species)
Wurch Mouse	*Muriculus imberbis*

Rattus, *Nesokia* and *Apodemus* all belong to essentially non-African murine groups. *Mus domesticus* (also called *Mus musculus*) is also a human commensal immigrant. However, the genus *Mus* is no stranger to Africa and an ancestral *Mus* is thought to have arrived here about 3 mya and has radiated since into some 20 species. Among these derivatives might be the rare and highly specialised *Muriculus imberbis*.

Two species of *Rattus* and several distinctly different populations of black rat have found their way to Africa. For both species their region of ultimate origin is South-East Asia. Only *Rattus rattus* is profiled here because it is the only species that has habituated to non-anthropogenic habitats and is of the greatest economic as well as biological and medical importance.



Black Rat

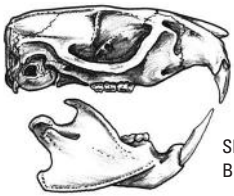
BLACK RAT *Rattus rattus*

MEASUREMENTS HB 133–180mm. T 180–209mm. W 100–186g.
RECOGNITION A long-tailed, coarse-haired athletic rat, usually black or dark grey with brownish tints on the back, but tints vary from population to population. Ears are large and mobile, face conical and deep-jawed.
HABITAT Still mostly in houses and stores but traps well away from villages are beginning to catch this species, implying that habituation to wild habitats is already under way. *R. rattus* fleas are the principal carrier of plague bacillus and, following the rat's arrival in Uganda, 60,000 people died of plague between 1917 and 1942 (a small and well-documented sample of a continent-wide catastrophe for humans).
FOOD Wholly omnivorous.
STATUS A pest and a dangerous disease vector. Also a valuable laboratory animal and sometimes pet.

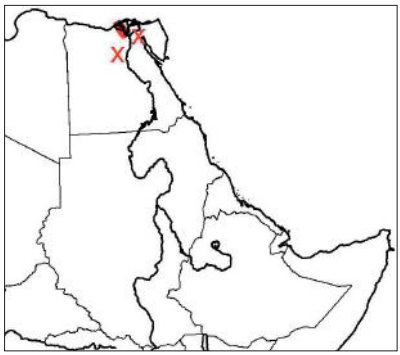
SHORT-TAILED BANDICOOT RAT

Nesokia indica

OTHER NAMES Egyptian Pest Rat.
MEASUREMENTS HB 165–197mm. T 110–134mm. W 205–280g.
RECOGNITION A hefty, dark-brown rat with shaggy hair and relatively small ears. Underside slightly lighter than upper, grey. Face blunt with prominent teeth.



Short-tailed Bandicoot Rat

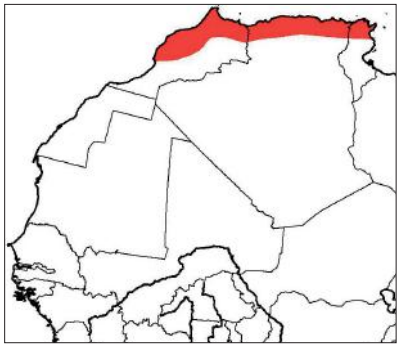


Short-tailed Bandicoot Rat

HABITAT Now almost entirely fields, canal banks and with a marked preference for wetter spots in an otherwise arid environment.
FOOD Caches various, mostly cultivated, roots, seeds and vegetables in 'stores' within burrows.
STATUS An agricultural pest.

LONG-TAILED FIELD MOUSE *Apodemus sylvaticus*

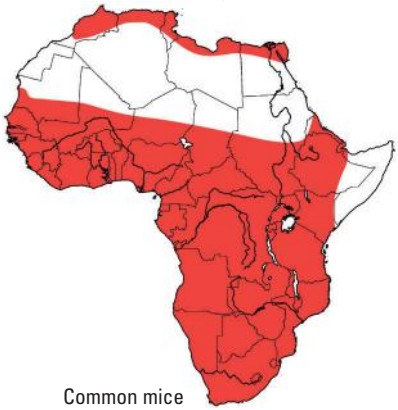
OTHER NAMES Wood Mouse.
MEASUREMENTS HB 80–105mm. T 70–115mm. W 13–30g.
RECOGNITION Large ears and eyes, and long hindlegs. Upperparts are brown with sandy flanks. Underparts are greyish white. It is normally absent from open areas.
HABITAT Restricted to the Mediterranean zone in N Africa, where it is common in all wooded and bushy areas, from sand dunes by the sea to high-altitude cedar forests.
FOOD Omnivorous: seeds, fruits, fungi, invertebrates.
STATUS Widespread along the Mediterranean littoral.



Long-tailed Field Mouse

COMMON MICE *Mus*

MEASUREMENTS HB 45–110mm. T 35–100mm. W 2.5–18.0g.
RECOGNITION A very variable group of mice, all bearing some resemblance to the Common House Mouse (*Mus musculus*). Proportions of visible features, i.e. tail, ears, muzzle, hands and feet, as well as skull form and teeth, serve to distinguish different species but the taxonomy and phylogeny of *Mus* is a work in progress. *M. spretus* on the Mediterranean is a close relative of *M. musculus* and both species are outside an older radiation within Africa. Several provisional groupings have been attempted, with the most widespread and



Common mice

M. minutoides

M. musculoides

successful species, *M. minutoides*, *M. musculoides* and *M. triton* emerging as the most recently evolved. Two mice, *M. bufo* in central Africa and *M. mahomet* in Ethiopia, probably represent mountain-adapted relicts of earlier populations.

SPECIES *M. baoulei*, *M. bufo*, *M. callewaerti*, *M. goundae*, *M. haussa*, *M. indutus*, *M. mahomet*, *M. mattheyi*, *M. minutoides*, *M. musculoides*, *M. musculus*, *M. neavei*, *M. orangiae*, *M. oubanguii*, *M. setulosus*, *M. setzeri*, *M. sorella*, *M. spretus*, *M. tenellus*, *M. triton*.

HABITAT Almost all vegetation types and all altitudes. Mice conceal themselves in every type of nook and cranny, dig burrows in various types of soil and gnaw holes in vegetation and buildings. They shred material to make substantial nests.

FOOD Omnivorous but individual species are likely to be dietary specialists to some extent.

STATUS Mostly little known.

WURCH MOUSE *Muriculus imberbis*

OTHER NAMES Ethiopian Striped Mouse.

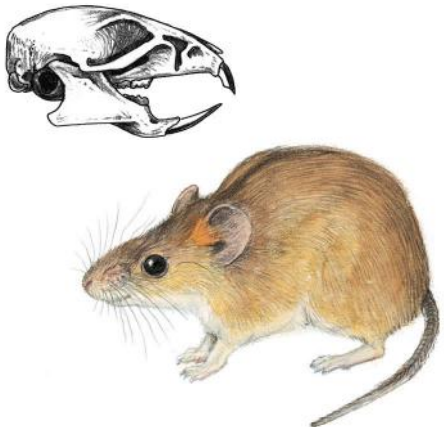
MEASUREMENTS HB 70–95mm. T 45–60mm. W (est.) 12–25g.

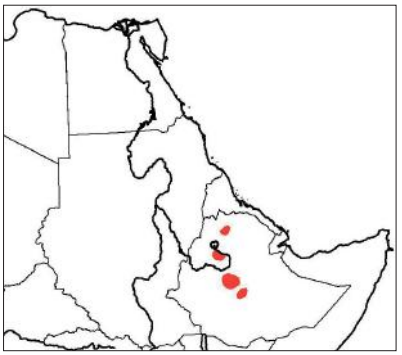
RECOGNITION A small, short-faced mouse with crisp, dense fur, blue-grey with yellow-brown tips. The lower back is marked by a black dorsal stripe. Underparts are yellowish to creamy white.

HABITAT Known from Ethiopian mountains between 1,900 and 3,400m in subalpine grassland (*Woina dega*) and heather/*Hypericum* moorlands (known locally as 'wurch'). The Wurch Mouse lives in holes, supposedly self-dug with mole-rat-like incisors. Reported associating with grass rats (*Arvicanthis* spp.).

FOOD Diet not known, perhaps seeds, but narrow, forward-pointing incisors could imply invertebrates too.

STATUS Rare, localised and declining in face of settlement. Vulnerable.





Wurch Mouse

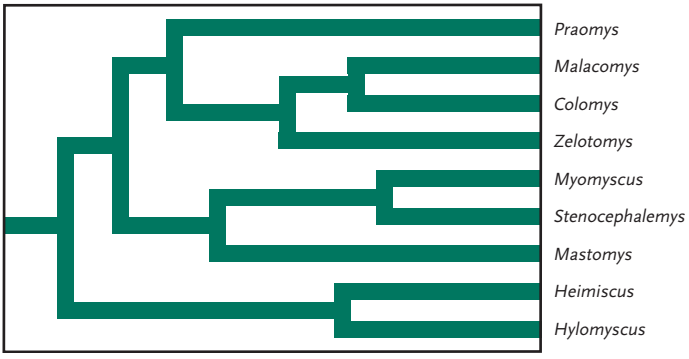
AFRICAN OMNIVOROUS MURINES (omni-murines)

Meadow mice	*Myomyscus* ('*Myomys*') (2 species)
Soft-furred rats	*Praomys* (species number uncertain)
Long-footed rats (Swamp rats)	*Malacomys* (5 species)
Velvet rats	*Colomys* (2 species)
Broad-headed stink rats	*Zelotomys* (2 species)
Multimammate rats	*Mastomys* (9 species)
Ethiopian meadow rats	*Stenocephalemys* (4 species)
De Balsac's Mouse	*Heimyscus fumosus*
African wood mice	*Hylomyscus* (species number uncertain)

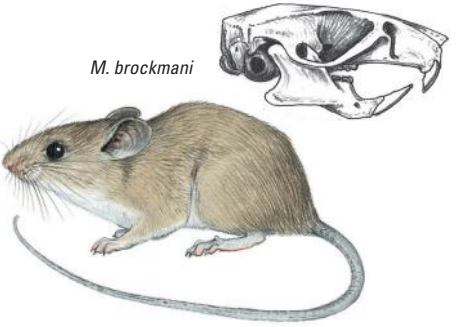
Recent genetic studies have helped make the broad outlines of a radiation by omnivorous murines somewhat clearer than before but many details remain obscure. A single, rather generalised, ancestral species is presumed to have entered Africa about 10.5 mya. Its advantages were a high and sustained level of activity, possibly superior disease resistance and greater potential for aggression, and exceptional ecological adaptability. Those adaptive strengths permitted the ancestral stock to spread into virtually all regions and radiation within Africa reflects subsequent adaptive refinements by countless local populations. Specific adaptive trends then developed which have geographic, ecological and physiological dimensions.

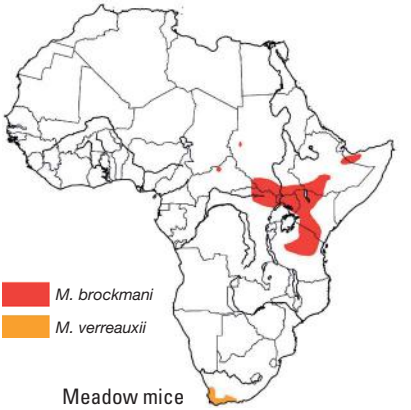
The ecological reach of the earliest omni-murines is manifest in locally endemic species occupying many outlying habitats, such as Ethiopia's tundras, the Cape's fynbos and various equatorial mountain heights. In Ethiopia *Stenocephalemys* represents a localised radiation. In the Cape the isolated *Myomyscus verrauxi* has become a local endemic, as have many other, less extreme, endemics. As non-forest murines, ancestral omni-murines had to adapt to the many challenges of equatorial rainforests. The wastepaper-basket taxa *Myomyscus* (formerly *Myomys*), *Praomys* and *Mastomys* are so generalised that it took today's genetic revolution to reveal that they sample populations that survive (sometimes little changed) from past eras. The *Praomys* basket in particular has overflowed with relicts from early stages in the evolution of specialisation and of local endemism*: P. obscurus* and *P. hartwigi* have become mountain specialists in West Africa and *P. degraffi* in central Africa; '*Praomys*' *delectorum* illustrates how diminished body size has favoured a shift into the lightweight arboreal niche and molecular genetics has now demonstrated that *'P.' delectorum* is closer to the arboreal wood mice, *Hylomyscus*, than it is to other soft-furred mice. *Hylomyscus* represents the culmination of this trend within the omni-murine radiation. Recent genetic phylogenies have suggested that *'Heimyscus' fumosus* and '*Mastomys*' *pernanus* also illustrate intermediate populations in the same trend towards arborealism. (The quotation marks serve to underline the uncertainties, even inadequacies, of nomenclature in this group of murines.)

Omni-murine specialisation reaches a climax in the velvet rats (or African water rats) *Colomys* adopting an aquatic lifestyle. This instance of an extreme adaptive shift illustrates evolution as a living, tangible process! The breadth and range of local niches that omni-murines have colonised are testament to their exceptional fitness.



Tentative phylogenetic tree for omnivorous murines (in part after Fabre *et al.* 2012).





Meadow mice

MEADOW MICE *Myomyscus* (‘*Myomys*’)

MEASUREMENTS HB 90–125mm. T 115–175mm. W 22–54g.

RECOGNITION Similar to soft-furred and multimammate rats: differences concern skull, teeth and chromosomes. The previous edition of this guide described meadow mice as ‘*Myomys*’, with six species. Because that name has now been pronounced invalid, taxonomists have re-examined former *Myomys* species, allocating most to other genera. *Myomyscus*, a resuscitated genus, serves as holder for two specialists that cannot be allocated with confidence to any other omni-murine genus. In another revision by specialists, ‘*Praomys*’ *fumatus*, which plausibly exemplified an ancient form of *Praomys*, is now *M. brockmani*.

SPECIES *M. brockmani* (syn *M. fumatus*), *M. verreauxii*.

HABITAT *M. brockmani*, ‘Panya Jiwe’ or ‘Stone Rat’ has a strong preference for rocky broken ground in eastern Africa. The very isolated species *M. verreauxii* is also found in stony terrain under extremes of heat and cold in fire-ravaged heather- and *Protea*-dominated fynbos.

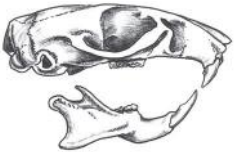
FOOD Insects and seeds collected on the ground at night.

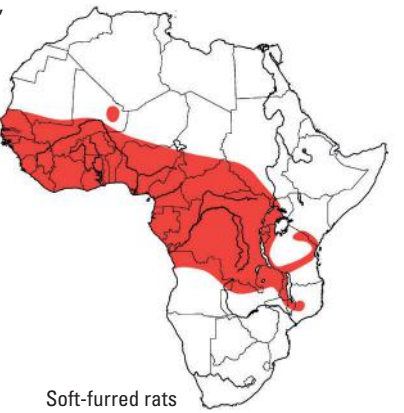
STATUS Conservative omni-murines living in challenging habitats.

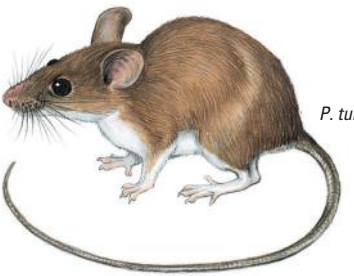
SOFT-FURRED RATS *Praomys*

MEASUREMENTS HB 90–150mm. T 100–170mm. W 30–50g.

RECOGNITION Generalised rats with short, soft fur, a long tail and large, round ears. They have brown or grey upperparts and paler underparts. The common ancestor to all omni-murines would have closely resembled both *Praomys* and *Myomyscus*, indeed, the very generalised rat ‘*Myomys daltoni*’ in the first edition of this guide is now *Praomys daltoni*. A more anomalous species, the ‘Delicate Mouse’, remains in *Praomys* in both editions. ‘*P.’ delectorum*, like *Heimyscus fumosus*, probably merits a separate generic name. Likewise, the taxa *lukolelae* and *verschureni* have both *Praomys* and *Malacomys* features, demonstrating that nomenclature can only


P. daltoni


Soft-furred rats


P. tullbergi

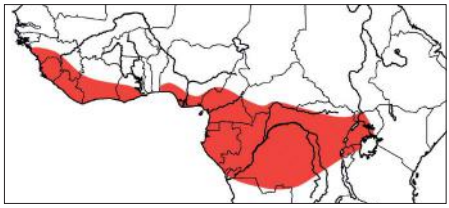
try to put names to the dynamics of adaptation among actively evolving mammals. *Praomys* has evolved, almost entirely, within the equatorial forests of the centre–west realm; its later-evolved species, *P. jacksoni*, *P. tullbergi* and *P. daltoni*, are all extremely successful and abundant. (A commensal form of *P. daltoni*, *P. derooi*, had probably anticipated many features of *Rattus rattus* behaviour before the Black Rat's arrival.)

SPECIES (groupings provisional) *Tullbergi* Group: *P. misonnei*, *P. rostratus*, *P. petteri;* West African montane isolates *P. obscurus*, *P. hartwigii*; Bioko Island isolate *P. morio*. *Jacksoni* group: *P. minor*, *P. degraaffi*, *P. mutoni*. *Daltoni* group: *P. derooi*. *P. delectorum* (close to *Hylomyscus*).

HABITAT Tropical forests, woodlands, moist savanna–forest mosaics and montane areas from Gambia to the Indian Ocean. Humid, heavily shaded forest floor or secondary scrub is preferred.

FOOD Omnivorous: invertebrates, fruits, seeds and leaves.

STATUS A genus subject to current revision and research.



Long-footed rats

M. longipes

LONG-FOOTED RATS (SWAMP RATS) *Malacomys*

MEASUREMENTS HB 120–180mm. T 140–210mm. W 50–150g.

RECOGNITION Long-legged, short-furred rats with large ears and a conical muzzle. Eyes are surrounded by a black 'mask'. The colour of the upperside varies from deep brown to grey, graduating to a lighter underside. *M. lukolelae/verschureni* resemble *Praomys* while *M. cansdalei* has many *Colomys*-like features, notably velvet-textured fur, sharper tonal contrast between upper side and under parts as well as cranial resemblances.

SPECIES *M. cansdalei*, *M. edwardsi*, *M. longipes*, *M. lukolelae*, *M. verschureni*.

HABITAT Very moist forest floor close to streams and swamps under a closed canopy; prefers ginger and arrowroot undergrowth. *Malacomys* species have a tropical range from Guinea to Uganda and L. Tanganyika.

FOOD Invertebrates and vegetable matter (fruits, seeds and roots); occasional small vertebrates.

STATUS Poorly known but *M. longipes* is widespread and common.

VELVET RATS *Colomys*

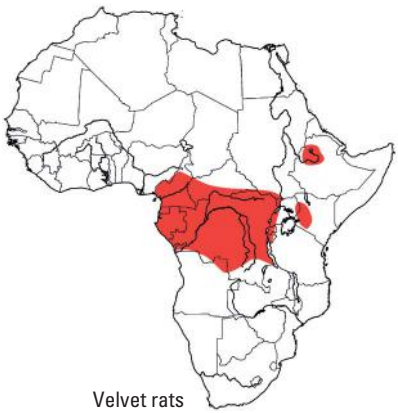
OTHER NAMES African water rats.

MEASUREMENTS HB 115–140mm. T 145–180mm. W 50–75g.

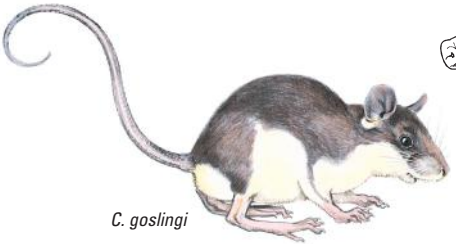
RECOGNITION Long-limbed, long-tailed rats with swollen rhinarium and profuse whiskers. The dense, velvet-textured fur is chocolate-brown above, pure white below. There is a white flash at the base of the ear. The chest glands of sexually active females exude a yellowish secretion. The describer of the larger Ethiopian species, known from a single locality, named it *Nilopegamys plumbeus*.

SPECIES *C. goslingi*, *C. plumbeus*.

HABITAT Margins of forest streams and swamp forests among palms, gingers and arrowroots; may follow narrow permanent river courses out of



Velvet rats

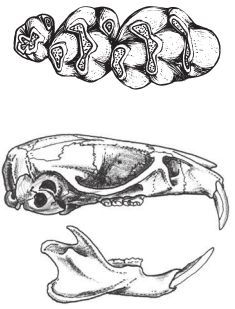

C. goslingi

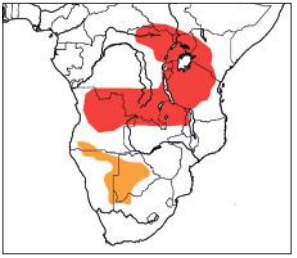
C. goslingi

forest. Ranges from Cameroon to W Uganda, Angola to L. Tanganyika, and is found along montane forest streams in Kenya and Ethiopia. The closely related *Malacomys cansdalei* occupies a comparable niche in Upper Guinea.

FOOD Aquatic insects, worms, slugs and crustaceans; occasionally vegetable matter.
STATUS Widespread in Congo basin, where not endangered, but very localised in Kenya. *C. plumbeus* restricted to Ethiopia.

Z. hildegardeae




Broad-headed stink rats

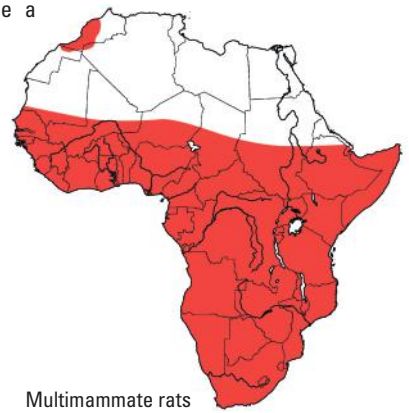
Z. hildegardeae
Z. woosnami

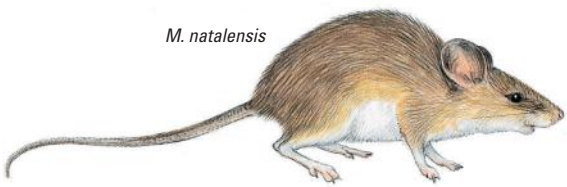
BROAD-HEADED STINK RATS *Zelotomys*

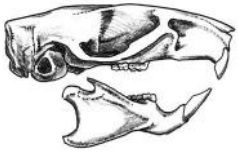
MEASUREMENTS HB 115–140mm. T 85–115mm. W 50–65g.
RECOGNITION Broad-headed rats with grey-brown or flecked grey upperparts and pale grey to white underparts and cheeks. Tail and limbs are off-white. Upper incisors are very protuberant. These rats have a very strong and (to human and perhaps other potential predator noses) disagreeable smell.
SPECIES *Z. hildegardeae* (E Africa and S Congo basin, in woodlands); *Z. woosnami* (central Kalahari).
HABITAT Southern and East Africa, in arid and semi-arid (*Z. woosnami*) or grassy savannas and scrub dominated by sword grass, *Imperata*.
FOOD Invertebrates, notably myriapods (*Z. hildegardeae*). *Z. woosnami* takes more seeds. Digestive adaptation to difficult foods such as poisonous myriapods, and incorporation of complex chemicals might be a significant strand in their biology.
STATUS Poorly known. Records very scattered.

MULTIMAMMATE RATS *Mastomys*

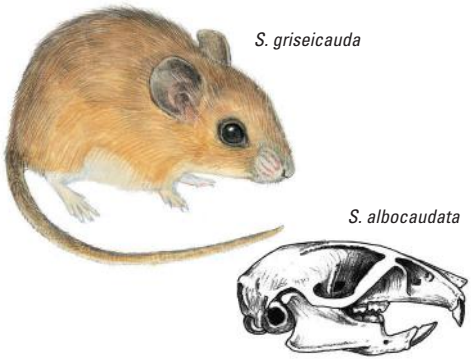
MEASUREMENTS HB 60–160mm. T 50–150mm. W 12–70g.
RECOGNITION Typical unspecialised rats with short, soft fur, a grey, brown or yellow upperside and a pale grey underside. The tail is usually shorter than the body. Females have 8–12 pairs of mammae. They are exceptionally fecund (6–22 young have been recorded). A relatively late but exceptionally successful spread through almost all the drier habitats of sub-Saharan Africa.

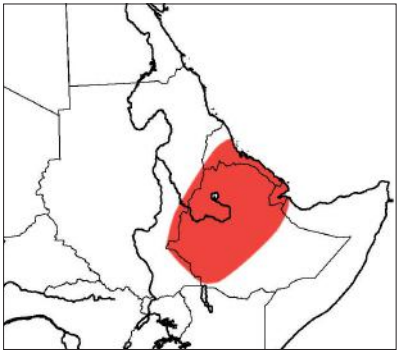

Multimammate rats




M. natalensis

SPECIES *M. angolensis*, *M. awashensis*, *M. coucha*, *M. erythroleucus*, *M. huberti*, *M. kollmanni-spergeri*, *M. natalensis*, *M. pernanus*, *M. shortridgei*.
HABITAT Savannas, woodlands, secondary growth, forest clearings, houses and fields in all but the driest areas of sub-Saharan Africa.
FOOD Fruits, seeds, invertebrates and household debris.
STATUS The classic 'multimammates' (*M. coucha* and *M. natalensis*) are well known (especially as dangerous disease vectors), the remainder less so.




Ethiopian meadow rats

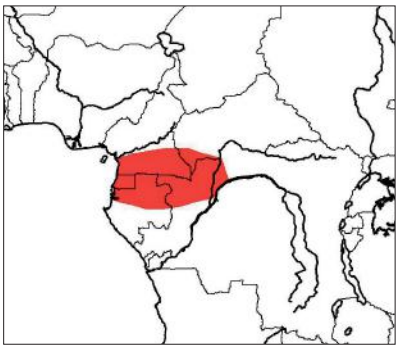
ETHIOPIAN MEADOW RATS *Stenocephalemys*

MEASUREMENTS HB 131–164mm. T 137–175mm. W 59–130g.
RECOGNITION Very large-headed rats with flimsy limbs and long, soft fur, dark grey at the base and tipped with orange. (Specialised montane isolates from early omni-murine stock.)
SPECIES *S. albipes*, *S. albocaudata*, *S. griseicauda*, *S. ruppi*.
HABITAT Ethiopian high-altitude endemics. These rats inhabit the afroalpine meadows and moorlands at 2,400–4,050m above sea level. They make burrows in short grass, everlasting brush (*Helichrysum*) and *Alchemilla* meadows (*S. albocaudata*). Also *Hypericum* scrub growing at slightly lower altitudes (*S. griseicauda*).
FOOD Omnivorous.
STATUS Abundant within restricted ranges.

DE BALSAC'S MOUSE

Heimyscus fumosus

OTHER NAMES African Smoky Mouse.
MEASUREMENTS HB 81–105mm. T 88–108mm. T 13–28g.
RECOGNITION A long-tailed, soft-furred mouse intermediate between *Hylomyscus* (originally described under that name) and *Praomys*.
HABITAT Rainforest between the Bight of Benin and the Congo R.

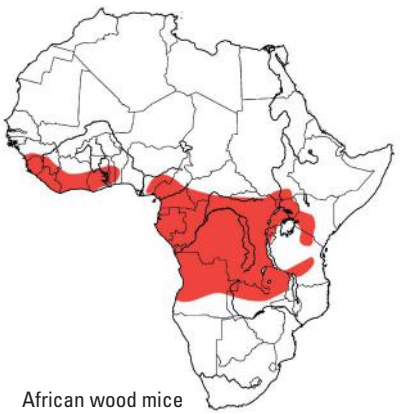

De Balsac's Mouse

De Balsac's Mouse

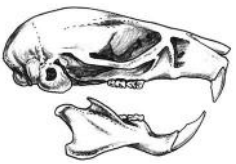
FOOD Invertebrates and seeds/fruits (in roughly equal proportions.
STATUS Generic status possibly unwarranted or in need of revision in a broader context.

AFRICAN WOOD MICE *Hylomyscus*

MEASUREMENTS HB 70–120mm. T 100–175mm. W 8–42g.
RECOGNITION Small arboreal mice with large, round ears, a long, thin tail and slender hands and feet. The grey-based fur has warmer-coloured tips in some species. These mice have a bright russet or orange back, a pale grey or white underside and a dark mask around the eyes. They are strictly nocturnal.
SPECIES *H. aeta*, *H. alleni*, *H. baeri*, *H. carillus*, *H. denniae*, *H. grandis*, *H. parvus*, *H. stella*. (*Praomys delectorum* might merit transfer to *Hylomyscus*.)
HABITAT Lowland and montane rainforests, afroalpine and subalpine moorlands (*H. denniae*) and secondary growth. Nests are made in holes and crevices and in the frond axils of palms and banana trees. *Hylomyscus* species have an equatorial distribution from Guinea to the East African mountains.
FOOD Omnivorous: fruits, seeds and insects.
STATUS Some species, i.e. *H. carillus*, *H. baeri*, *H. grandis*, are highly localised.



African wood mice

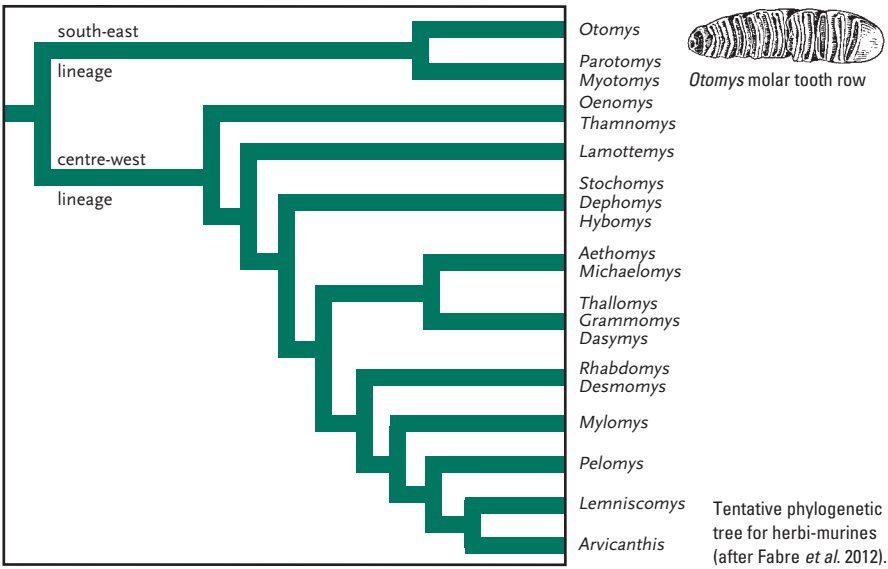


H. stella

H. stella

AFRICAN HERBIVOROUS MURINES (herbi-murines)

Herbivorous murines in Africa derive from a rat-like (and probably omnivorous) ancestor coming in from Eurasia about 10.5 mya. The first murine colonists to reach southern Africa found climatic conditions similar to the temperate Mediterranean of their immediate origins. By 4.5 mya a South African fossil, *Euryotomys*, still combined dental traits of a generalised murine with the dental laminae typical of grass-eating rats. An early commitment to a wholly herbivorous diet thereafter led the groove-toothed rats, Otomyini, to evolve some striking convergent similarities with two unrelated murids: voles *Arvicola*, in Eurasia and cotton rats, *Sigmodon*, in America. The end product of this mainly southern (and later, eastern) African radiation has been a rather uniform, highly specialised group, now generally recognised as Otomyini (but so distinctive it was once classed as a family!). It consists of stocky, shaggy, blunt-faced rats with short legs, a short tail and rounded ears. The skull is robust and most species have grooved upper incisors. The cheek-teeth have mill-like laminations.



Otomys molar tooth row

Tentative phylogenetic tree for herbi-murines (after Fabre *et al.* 2012).

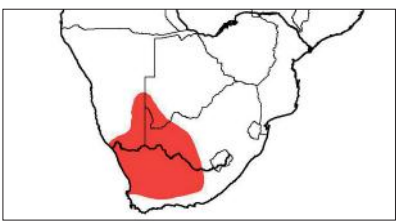
An important biogeographic implication of the split between otomyins and the other herbi-murines is that the mainstream branch of herbi-murines probably first evolved within the equatorial centre–west realm. By contrast, Otomyini first evolved in the temperate reaches of the south–east realm. Therefore the herbi-murine split into two major divisions conforms with a primary continental divide that has governed the evolution of other biota.

AFRICAN HERBIVOROUS MURINES (south-east lineage: Otomyini)

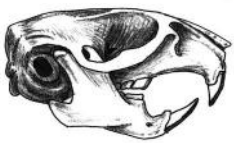
Whistling rats	*Parotomys* (2 species)
Cape ice rats	*Myotomys* (2 species)
Groove-toothed rats	*Otomys* (13 species)

WHISTLING RATS *Parotomys*

MEASUREMENTS HB 120–170mm. T 80–120mm. W 90–155g.
RECOGNITION Shaggy, large-eyed, short legged, diurnal rats of variable colouring from fawn to grey-brown (paler than *Otomys*). Often inhabit individual territories within quite tight clusters, where they whistle loudly, often from an upright, seated position at the burrow entrance.

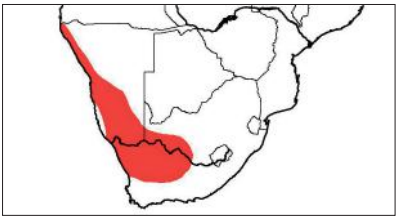


Brants's Whistling Rat



P. littledalei

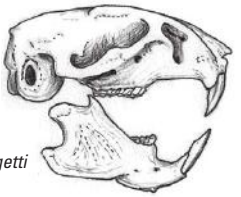
SPECIES Brants's Whistling Rat (*P. brantsii*): upper incisors ungrooved. Littledale's Whistling Rat (*P. littledalei*): upper incisors grooved.
HABITAT Dry, sandy environments in SW Africa where both species excavate burrows.
FOOD Grass stems and seeds. Stems and leaves of xerophytic shrubs.
STATUS Locally abundant.



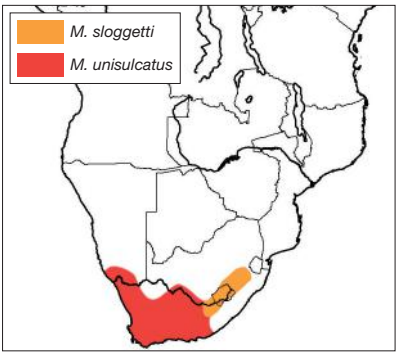
Littledale's Whistling Rat

CAPE ICE RATS *Myotomys* (formerly *Liotomys*)

OTHER NAMES Sloggett's Vlei Rat and Karoo Vlei Rat.
MEASUREMENTS HB 93–205mm. T 47–106mm. W 45–156g.
Two rats from cold Cape habitats. Usually included in *Otomys* but genetically occupy an intermediate position closer to *Parotomys* than to *Otomys*. *M. sloggetti*, in particular, is a fine-coated rat with russet muzzle, relatively large eyes and small ears.
SPECIES *M. sloggetti*, *M. unisulcatus*.
HABITAT Cape fynbos and Karoo.
FOOD Forage on the ground as well as arboreally, mainly for leaves and fruits. Food is eaten on the spot while abundant but stored in the winter.
STATUS Unusually tame; locally abundant.



M. sloggetti

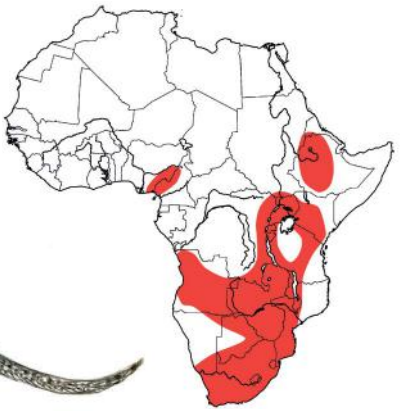


Cape ice rats

M. sloggetti

GROOVE-TOOTHED RATS *Otomys*

OTHER NAMES Vlei rats.
MEASUREMENTS HB 120–220mm. T 60–120mm. W 100–260g.
RECOGNITION Shaggy rats of very varied colouring (but usually dark) with a very blunt muzzle and large ears. Upper incisors are always grooved (similar *Dasymys* has plain incisors). Very placid, they give birth to precocious young.
SPECIES *O. anchietae*, *O. angoniensis*, *O. barbouri*, *O. burtoni*, *O. cuanzensisa*, *O. denti*, *O. irroratus*, *O. lacustris*, *O. laminatus*, *O. occidentalis*, *O. saundersiae*, *O. tropicalis*, *O. typus*.



Groove-toothed rats

O. typus

O. irroratus

O. tropicalis

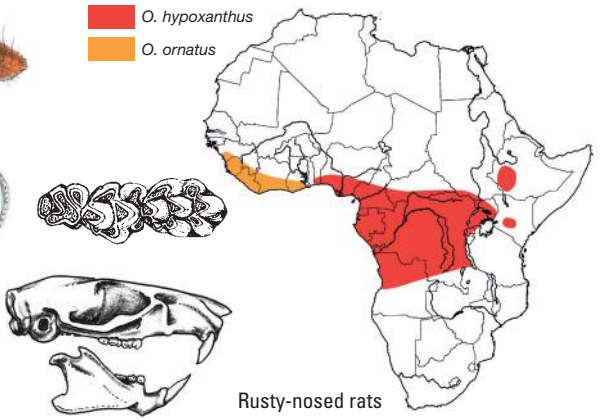
HABITAT Grasslands, marshes, dense secondary growth, tangles and open savanna, especially at higher altitudes. Some species may have become 'relicts' because they originally adapted to moist, fire-less regimes that pre-date landscapes fired and cultivated by humans. Their distributions are therefore discontinuous, mainly eastern upland and southern temperate.
FOOD Green grass, reed and herb stems, bark, seeds and flowers; occasionally roots and fruits.
STATUS Some species have limited ranges.

AFRICAN HERBIVOROUS MURINES (mainstream herbi-murines)

Rusty-nosed rats	*Oenomys* (2 species)
Mount Oku Rat	*Lamottemys okuensis*
Broad-footed thicket rats	*Thamnomys* (3 species)
Hump-nosed mice	*Hybomys* group (6 species)
Dephua Rat	*Dephomys defua*
Target Rat	*Stochomys longicaudatus*
Bush-rats	*Aethomys* (9 species)
Namaqua rock mice	*Micaelamys* (2 species)
Acacia rats	*Thallomys* (4 species)
Narrow-footed thicket rats	*Grammomys* (11 species)
Shaggy swamp rats	*Dasymys* (5 species)
Four-striped Grass Mouse	*Rhabdomys pumilio*
Dega rats	*Desmomys* (2 species)
Creek rats	*Pelomys* (5 species)
Mill rats	*Mylomys* (2 species)
Zebra mice	*Lemniscomys* (11 species)
Grass rats	*Arvicanthis* (7 species)

The 'mainstream' lineage of herbi-murines embraces 17 very diverse but generally deep-jawed, tooth-modified, herbivorous genera. There are, perhaps, too many genera and further revisions in nomenclature and taxonomy are likely in the near future. They derive from an almost certainly omnivorous ancestor that entered Africa about 10.5 mya. This precursor might, or might not, have given rise to both omni-murines and herbi-murines. In either case, it should be noted that some herbi-murines have retained (or perhaps re-acquired) generalised traits, including a taste for animal matter in the diet. This need not surprise: already omnivorous, early murines (arriving via a semi-arid bridge or corridor) would have needed animal foods to survive dry seasons or periods.

What precipitated herbivory and where was it most likely to develop? Herbi-murines that are known to be the most genetically conservative are associated with continuous grass and herb re-growth within tropical high rainfall zones (notably *Oenomys*, *Lamottemys*, *Thamnomys*, *Stochomys* and *Dephomys*). Genera and species that evolved later suffer no such constraints and centre–west origins, as discussed earlier, have become overlaid by the striking ecological success of widespread species such as *Lemniscomys* and *Arvicanthis*. Nonetheless, herbi-murine origins seem most likely to have begun in the equatorial centre–west biogeographic realm.

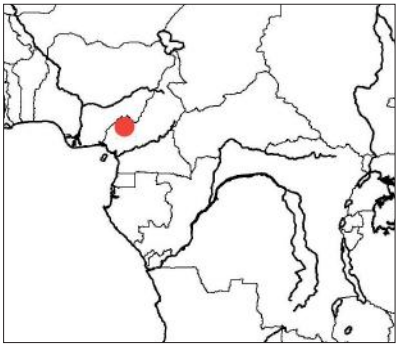


RUSTY-NOSED RATS *Oenomys*

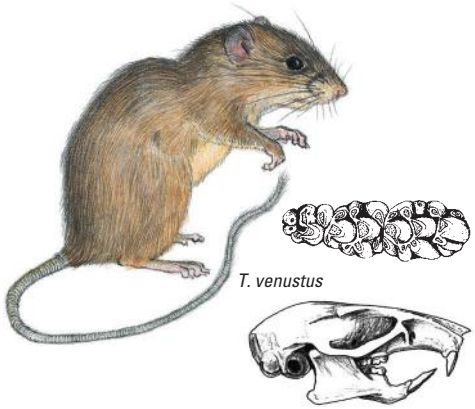
OTHER NAMES Rufous-nosed rats.
MEASUREMENTS HB 130–180mm. T 140–210mm. W 50–121g.
RECOGNITION Shaggy brown rats with a bright red or orange nose and rump. The fur is soft, with long guard hairs. The belly is white or pinkish, with a warm tinge to the margin with the darker fur. Semi-arboreal and nocturnal.
SPECIES *O. hypoxanthus*, *O. ornatus*.
HABITAT Forest belt from Guinea to central Kenya. Not true forest species but they favour secondary growth in clearings – road verges, chablis, clearings and margins of marshes, where they are commonest in sedge or elephant grass (*Pennisetum*) beds: (the latter typically grows wherever forests have been felled). Commonly nest in exotic Billy-goat Weed (*Ageratum conyzoides*).
FOOD Green leaves, stems, shoots, buds and green seeds; also insects.
STATUS Common.

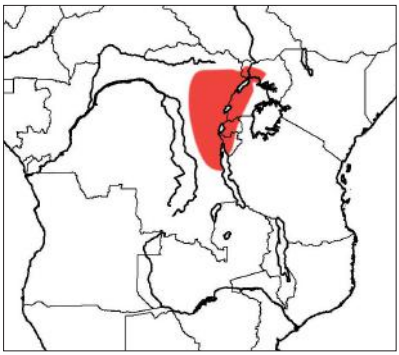
MOUNT OKU RAT *Lamottemys okuensis*

MEASUREMENTS Unavailable.
RECOGNITION A shaggy brown, semi-arboreal rat related to the rusty-nosed rats and broad-footed thicket rats.
HABITAT Secondary growth in montane habitats surrounding Mt Oku, Cameroon uplands. This rat is possibly the relict of a formerly widespread form of very early herbi-murine.
FOOD Thought to be herbivorous and to forage mainly on the ground
STATUS Rare, localised and little known.



Mount Oku Rat





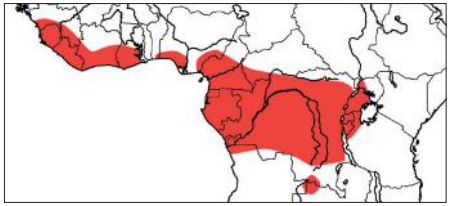
Broad-footed thicket rats

BROAD-FOOTED THICKET RATS *Thamnomys*

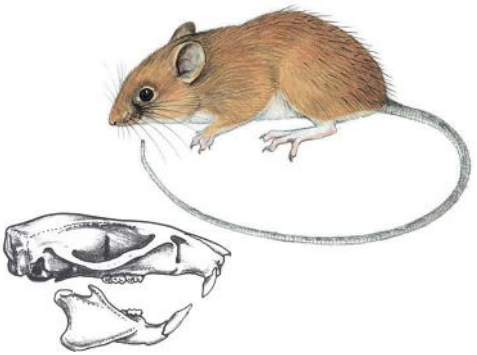
MEASUREMENTS HB 114–173mm. T 170–226mm. W 40–108g.
RECOGNITION Montane, mainly arboreal rats with broad feet and a long, lightly haired tail. The back is brown or rufous with soft grey underfur of a very dense, even texture. The underside is white or cream but soft and grey under paler hair-tips. The structure of the teeth suggests that *Thamnomys* are arboreal relatives of *Oenomys*, a relationship confirmed by genetics. Numerous convergences with *Grammomys* formerly led to much taxonomic confusion between the two.
SPECIES *T. kempi*, *T. venustus*, *T. schoutedeni*.
HABITAT Montane forests in E DR Congo, Uganda, Rwanda and Burundi.
FOOD Plant material, including leaves and seeds. Long digestive tract.
STATUS Rare relict species deriving from a very early herbi-murine lineage adapting to mainly arboreal herbivory.

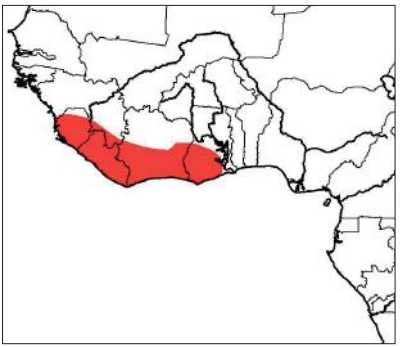
HUMP-NOSED MICE *Hybomys* group

OTHER NAMES Forest mice.
MEASUREMENTS HB 100–160mm. T 85–130mm. W (est.) 40–80g.
RECOGNITION Inconspicuous dark mice with stiff-textured fur, some finely freckled with black. The underfur is grey or brown. The arched profile of the head reflects the 'humped' shape of the skull in most species. Several species have intensely black shiny skin on the soles of the feet. These mice are both nocturnal and diurnal.
SPECIES *H. badius*, *H. basilii*, *H. lunaris*, *H. planifrons*, *H. trivirgatus*, *H. univittatus*. Sub-genera possible.
HABITAT Equatorial forests between Sierra Leone and the upper Nile. Strictly terrestrial, preferring areas with abundant leaf litter and heavy shade; known to shelter in rotting logs.
FOOD Fallen fruits, seeds, green leaves and insects (mostly termites and ants).
STATUS The genus is in need of revision.



Hump-nosed mice





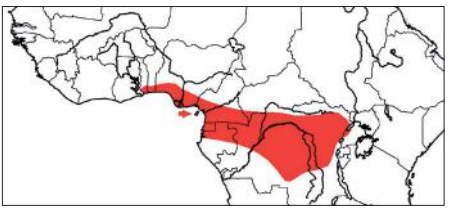
Defua Rat

DEFUA RAT *Dephomys defua*

MEASUREMENTS HB 115–135mm. T 180–205mm. W (est.) 40–65g.
RECOGNITION Arboreal rat with broad hindfeet, a very long tail and a long conical head with medium-sized oval ears. Back and flanks are reddish brown, sharply demarcated from the white belly. The fur is somewhat stiff in texture and has fine guard hairs projecting from the rump. Nocturnal.
HABITAT Secondary and swampy palm forests and secondary scrub in Upper Guinea forests, Sierra Leone to Ghana.
FOOD Mainly fallen fruit and other vegetable matter; also insects.
STATUS Widespread in Upper Guinea but not common.

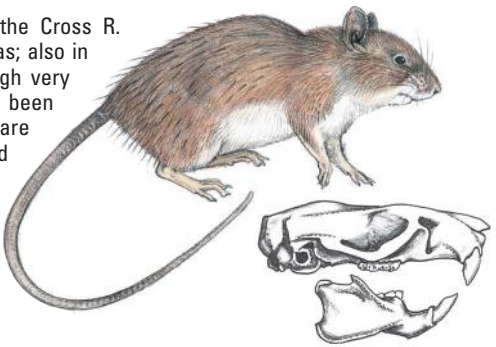
TARGET RAT

Stochomys longicaudatus



Target Rat

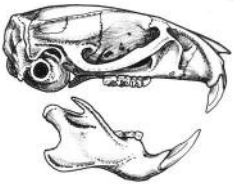
MEASUREMENTS HB 120–175mm.
T 185–250mm. W 50–104g.
RECOGNITION A dark, reddish forest rat that gets its name from the long black bristles on its rump, which have been likened to arrows. The pale-tipped belly hairs form a deep brown fur closer to the skin. The feet are off-white and the tail is long and finely tapered.
HABITAT Equatorial lowland forests from the Cross R. to W Uganda. Riversides and swampy areas; also in secondary growth around villages. Although very patchily distributed, aggregations have been found in oil-palm plantations. Target Rats are nocturnal and make round nests of shredded material.
FOOD Forages, mostly on the ground, for fruits, seeds and, possibly, some insects.
STATUS Wide distribution. The reasons for its irregular occurrence are not known.

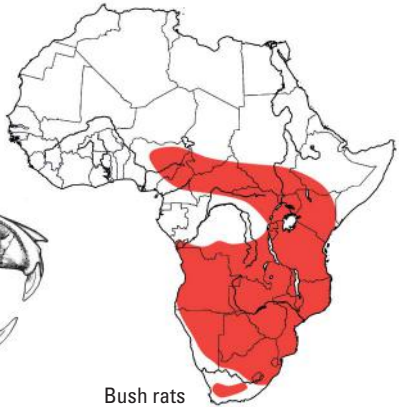


BUSH RATS *Aethomys*

OTHER NAMES Veld rats.
MEASUREMENTS HB 120–190mm. T 120–210mm. W (est.) 50–150g.
RECOGNITION Generalised rats with streaky-looking, soft fur of very variable colour (by species and region). The underside is paler and the ears are large and rounded. Body and tail are about equal in length. Derived directly from the earliest herbi-murines and with some species having a marked association with termite mounds, few species are common. *A. silindensis* and *A. bocagei*

A. kaiseri





Bush rats

are probably relictual pockets of earlier bush rat expansions. *A. kaiseri*, in the Great Lakes region and Congo/Zambezi headwaters region, is widespread but very rarely common. *A. hindei* may represent a somewhat later emergence, north of the Equator, from the same stock as *A. kaiseri*. *A. stannarius* is probably a western isolate of *A. hindei*. The most recently emerged species, *A. chrysophilus* (and its close, possibly ancestral, ally *A. ineptus*) range very widely south of the Equator.

SPECIES *A. bocagei*, *A. chrysophilus*, *A. ineptus*, *A. hindei*, *A. kaiseri*, *A. nyikae*, *A. silindensis*, *A. stannarius*, *A. thomasi*.

HABITAT Strong preference for rocky habitats in S and E Africa, with an outlying population in Nigeria (*A. stannarius*). Patchily common on cultivated land and close to termitaries, or on rough slopes.

FOOD Grass, stems, leaves and seeds.

STATUS An ambiguous taxon, once regarded as an African equivalent of *Rattus*. All species are of least conservation concern.

NAMAQUA ROCK MICE *Micaelamys*

MEASUREMENTS HB 80–147mm. T 107–197mm. W 28–88g.

RECOGNITION Long-tailed, large-eyed rats formerly included in *Aethomys,* but genetically very distinct. Back and rump streaky brown and black with yellowish or reddish cheeks, flanks and upper limbs, underside white.

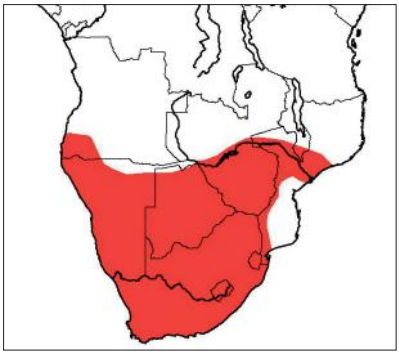
SPECIES *M. granti, M. namaquensis*.

HABITAT Fynbos, Karoo, high veld and other southern temperate habitats, very often on rocky ground. Distribution very roughly follows the 18° C Isotherm.

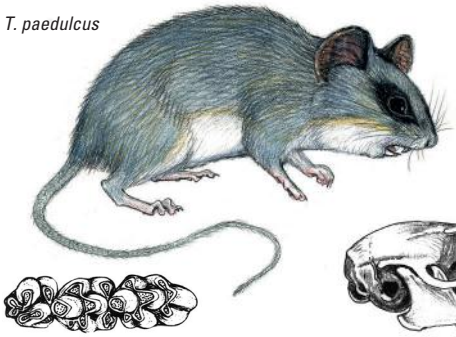
FOOD Nocturnal forager on grass, leaves, seeds and nectar. A sugar-bush, *Protea pudens*, flowers at ground level; *Micaelamys* is known to assist pollinating this species while visiting for nectar (and possibly for insects, a more occasional food).

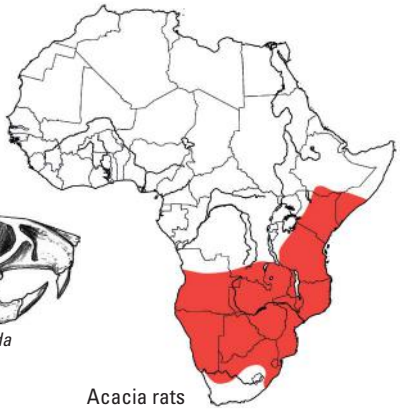
STATUS IUCN lists as of least concern.

M. namaquensis



Namaqua rock mice



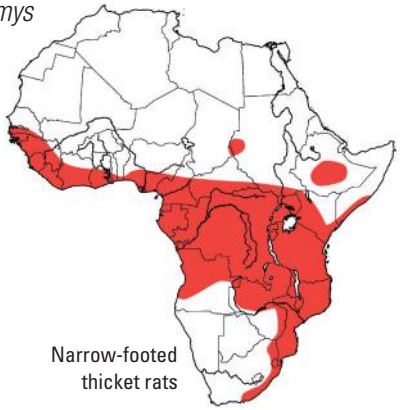

Acacia rats

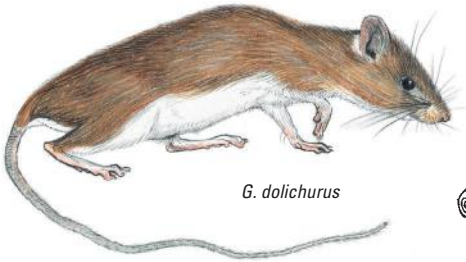
ACACIA RATS *Thallomys*

OTHER NAMES Tree rats.
MEASUREMENTS HB 117–160mm. T 127–210mm. W 50–85g.
RECOGNITION Arboreal rats with a long, slightly hairy tail, large, round ears and sharp, curved claws on short feet. The back is grey or brownish, underside white. Usually a bold black mask around the eyes. Some *Thallomys* species build thorned twig structures along branches and trunks and outside their nests. Such structures may be of seasonal occurrence. Presumably they function to deter predators and provide cover in an exposed and very dangerous savanna environment.
SPECIES *T. loringi*, *T. nigricauda*, *T. paedulcus*, *T. shortridgei*.
HABITAT Dry *Acacia*-dominated woodlands and savannas from South Africa to the Horn of Africa and Ethiopia. Acacia rats construct (unthorned) twig, leaf and grass nests in crevices, hollows or forks, as well as (thorned) twig 'corridors'. The preferred *Acacia* species are *A. erioloba*, *A. tortilis* and *A. xanthophloa*.
FOOD Forage almost exclusively in the acacias in which they live, nibbling off buds, young leaves and the skin of green pods. They also augment the natural acacia gum exudates they eat by wounding bark, this induces further resin flow. Their digestive tract is extensively modified to digest the extremely nutritious first growth of *Acacia* spp.. Reported to eat roots and insects occasionally.
STATUS The fortunes of *Thallomys* are inseparable from those of the *Acacia* species on which they live. Currently uncontrolled, scorched-earth charcoal burning (as practised near most large cities) eliminates them entirely. Substantial declines have also been noted after frequent firing in the vicinity of their trees.

NARROW-FOOTED THICKET RATS *Grammomys*

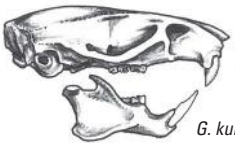
OTHER NAMES Thicket rats.
MEASUREMENTS HB 86–133mm. T 144–201mm. W 18–54g.
RECOGNITION Slender, arboreal mice with prominent, oval ears and a very long, finely haired tail. They have a brown, tan or grey back and pure white or creamy belly (differs by species and habitat). Guard hairs are present on the rump. These are


Narrow-footed thicket rats



miniature murine equivalents of squirrels, able to progress through dense vegetation with speed and dexterity. A scatter of species with localised, apparently relict ranges are strung out along the Equator. *G. kuru* occupies much of the centre–west forest realm, from the Nile in Uganda to Guinea. Even more widespread, *G. dolichurus* ranges over a large part of the south–east realm. *G. cometes* represents a southern isolate closely related to *G. dolichurus*. The genetic affinities of *G. macmillani* suggest links between *Grammomys* and *Thallomys*.

G. ibeanus



G. kuru

SPECIES *G. aridulus*, *G. buntingi*, *G. caniceps*, *G. cometes*, *G. dolichurus*, *G. dryas*, *G. gigas*, *G. ibeanus*, *G. kuru*, *G. macmillani*, *G. minnae*.

HABITAT Mainly moister tropical vegetation types from Guinea to the Indian Ocean coast. These range from forest undergrowth, bracken, reedbeds and grassy savannas to miombo woodlands. Convergent with the broad-footed thicket rats *Thamnomys*, with which it was once lumped.

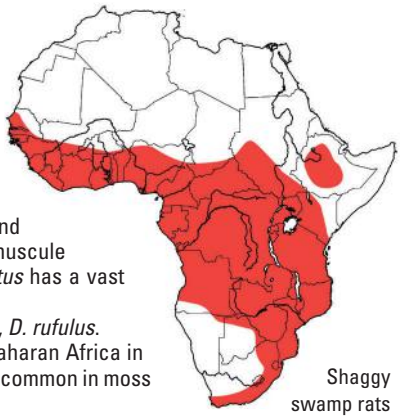
FOOD Fruits, seeds, stems and other vegetable matter; occasionally insects.

STATUS A *Grammomys*-specific malaria, to which the mice are largely immune, has been found to be deadly for laboratory rats and mice. This discovery has invested *Grammomys* with special interest as experimental animals.

SHAGGY SWAMP RATS *Dasymys*

MEASUREMENTS HB 130–205mm. T 93–186mm. W 45–218g.

RECOGNITION Robust, shaggy rats with a somewhat flattened, disc-like face, small eyes and rounded pink ears, almost lost in the dark brown fur. Underparts are pale brown-grey. The tail is shorter than the body. Incisors are plain orange. These rats derive from a very early offshoot of the *Arvicanthis/Lemniscomys* and *Pelomys* lineage. *D. foxi* and *D. montanus* have minuscule ranges. *D. rufulus* occupies Upper Guinea. *D. incomptus* has a vast range from Ethiopia to the Cape.



Shaggy swamp rats

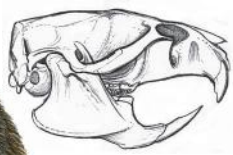
SPECIES *D. foxi*, *D. incomptus*, *D. montanus*, *D. nudipes*, *D. rufulus*.

HABITAT Dense cover in wetter grassy areas of sub-Saharan Africa in marshes, including higher altitudes where they may be common in moss and sedge bogs. Swim well.

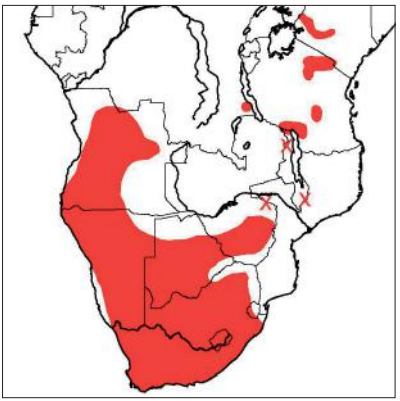
FOOD Stems, roots, shoots and flowers of plants, notably reeds and aquatic grasses in waterlogged habitats, including moss and rushes. Occasionally insects.

STATUS Only found in waterlogged areas so distribution very patchy. Regarded as a pest in rice paddies.

D. incomptus



D. incomptus

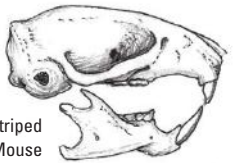


Four-striped Grass Mouse

FOUR-STRIPED GRASS MOUSE

Rhabdomys pumilio

MEASUREMENTS HB 99–124mm. T 71–101mm. W 41–53g.
RECOGNITION Grass mouse with four black stripes along its back, with two pale interstripes and a dorsal buff line in the centre. A compact mouse with relatively small ears, sometimes orange or red. Genetically, this species shares recent ancestry with *Desmomys*, which inhabits comparable habitats in Ethiopia.
HABITAT Limited to cooler grasslands in southern and south-western Africa and in a string of East African mountains; very discontinuous distribution.
FOOD Vegetarian: stems, leaves and seeds of grass.
STATUS Common in appropriate habitats.



Four-striped Grass Mouse

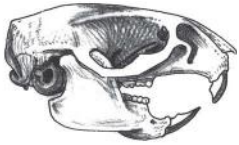
DEGA RATS *Desmomys*

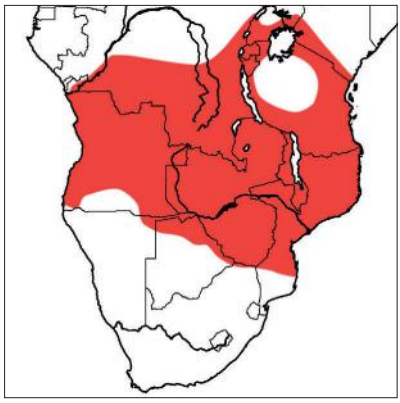
OTHER NAMES Scrub rats.
MEASUREMENTS HB 117–144mm. T 122–145mm. W 45–77g.
RECOGNITION Shaggy, blunt-faced rats with bold ochraceous flanks and a pure white belly. The molar teeth are mill-like but have their own pattern of lophs and cusps. Genetically very close to *Rhabdomys*.
SPECIES *D. harringtoni*, *D. yaldeni*.
HABITAT Ethiopian mountains between 1,500 and 3,000m (a zone locally known as 'dega'). They live among grasses in degraded juniper, *Podo* and *Hagenia* forests and in upland *Acacia* savannas.
FOOD Grass stems and leaves.
STATUS Locally abundant.

D. harringtoni

Dega rats

P. fallax





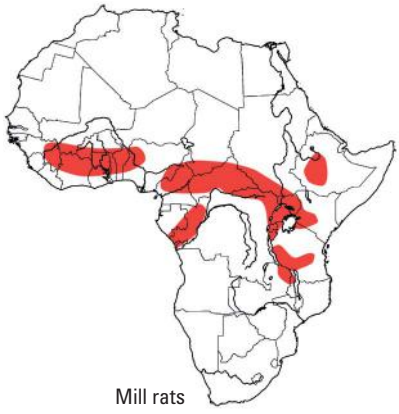
Creek rats

CREEK RATS *Pelomys*

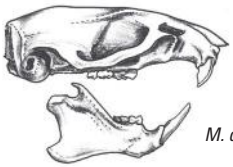
MEASUREMENTS HB 101–174mm. T 100–171mm. W 42–151g.
RECOGNITION Creek rats resemble grass rats, *Arvicanthis*, but have grooved incisors and a blunt face, with body and tail of similar length. Genetically very close to *Mylomys*. Glossy brown coat of longish, coarse fur in which ears partly hidden. Mainly nocturnal. Exclusive to south–east biogeographic realm.
SPECIES *P. campanae*, *P. fallax*, *P. hopkinsi*, *P. isseli*, *P. minor*.
HABITAT Associated with marshes, reedbeds, damp valley bottoms, lakeshores and mountain bogs in central and East Africa. They excavate burrows.
FOOD Grass and reed shoots, stems, leaves and seeds.
STATUS Locally common within appropriate habitats or region.

MILL RATS *Mylomys*

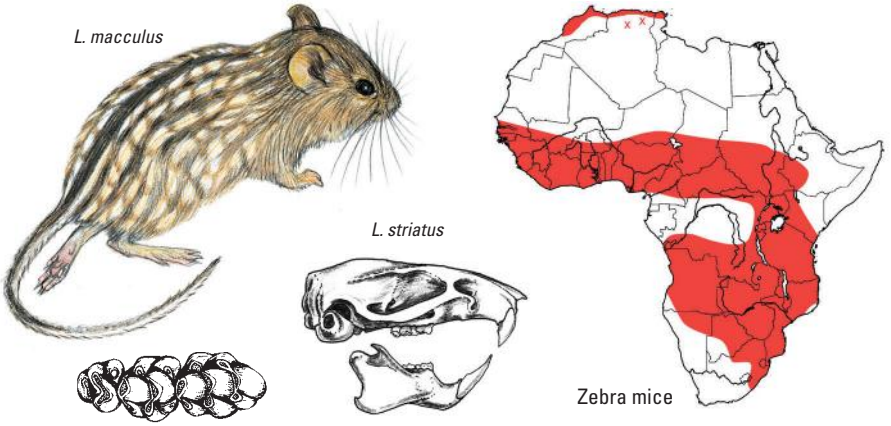
OTHER NAMES Three-toed grass rats.
MEASUREMENTS HB 120–190mm. T 100–180mm. W 46–165g.
RECOGNITION Named after their mill-like grinding molars, mill rats are externally, and genetically, very similar to creek rats. They have three functional digits on the forefeet, grooved incisors, shiny, streaked-brown upperparts and a white underside. The tail is conspicuously bicoloured.
SPECIES *M. dybowski*, *M. rex*.
HABITAT Tropical northern savannas from Guinea to W Kenya with *M. rex* in the Ethiopian highlands. Found in a variety of moist grasslands at altitudes of up to 2,500m, it is locally and discontinuously distributed. It is sometimes the commonest species in stands of sword grass (*Imperata*) and other mono-dominant grass types.
FOOD Green grass stems and leaves.
STATUS Locally abundant.



Mill rats

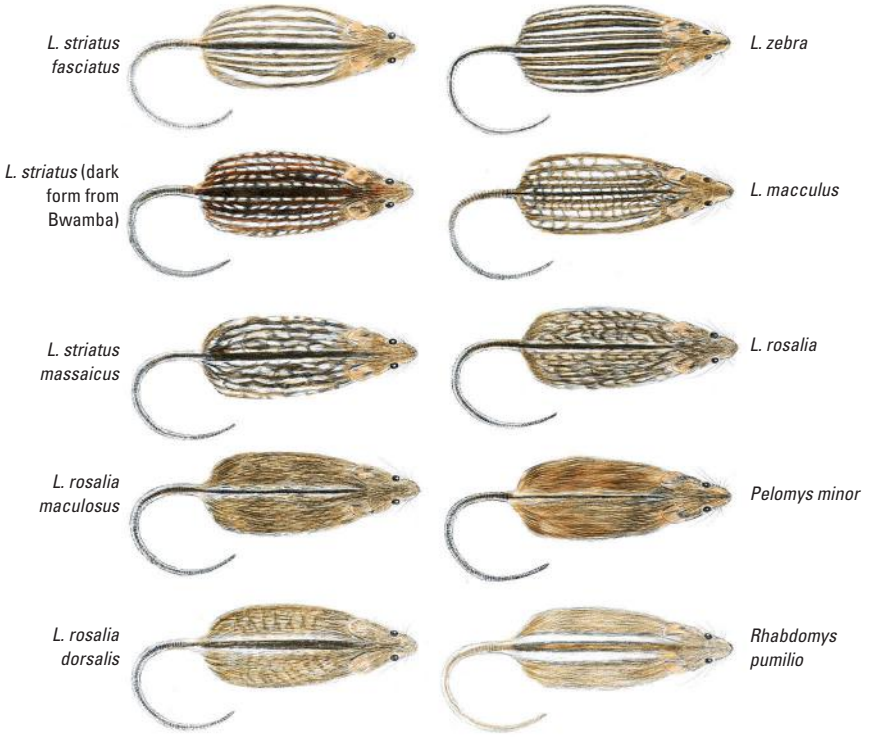


M. dybowski



ZEBRA MICE *Lemniscomys*

OTHER NAMES Grass mice.
MEASUREMENTS HB 90–140mm. T 95–150mm. W (est.) 18–70g.
RECOGNITION Mice with variable numbers of dorsal stripes, some with light unbroken lines, others fragmented into dashes. All have a near-black dorsal midline. An actively speciating genus, influenced, perhaps, by their relationship with anthropogenic firing of grasslands. Populations of some species decline in the absence of fire whereas they peak 3–10 months after a pasture has been burned. Genetic phylogenies have shown that *L. barbarus*, isolated north of the Sahara, is the



most conservative species, followed by *L. striatus*, the most widespread species. *L. zebra* is also among the older populations, followed by *L. rosalia*. Significantly, the genetically most recently evolved, *L. maculus* and *L. bellieri*, are both from once-wooded areas and habitats where human-induced, fire-climax grasslands have become extensive.

SPECIES *L. barbarus*, *L. bellieri*, *L. griselda*, *L. hoogstraali*, *L. linulus*, *L. macculus*, *L. mittendorfi*, *L. rosalia*, *L. roseveari*, *L. striatus*, *L. zebra*.

HABITAT African grasslands south of the Sahara (and one species, *L. barbarus*, in Morocco). The ranges of several species overlap and they partition the habitat in such areas but broaden their niches when free of competition. Very fecund, a single pair can produce four litters of up to 12 (usually four or five) young in less than 4 months.

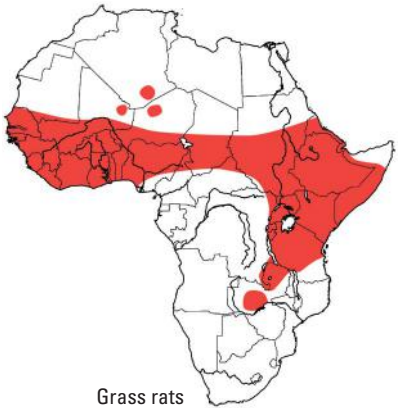
FOOD Grass stems, leaves and seeds. Insects are periodically taken.

STATUS Together with a few other diurnal tropical rodents, *Lemniscomys* brains are covered with black sun-block in the form of a melanin layer in the cranial periosteum. These pretty little mice are popular pets and zoo exhibits.

GRASS RATS *Arvicanthis*

MEASUREMENTS HB 84–238mm. T 70–170mm. W 48–258g.

RECOGNITION Robust grizzled grass rats with a harsh, brown, ochraceous or greyish coat. They have smooth incisors and distinctive, mill-like molars. Mostly diurnal and prone to frequent population explosions and crashes. This genus evolved relatively recently (first fossil at 1.5 mya) almost certainly originating in Ethiopia from the same parent stock as *Lemniscomys*.



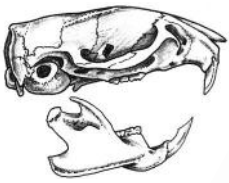
Grass rats

SPECIES *A. abyssinicus*, *A. ansorgei*, *A. blicki*, *A. neumanni*, *A. nairobae*, *A. niloticus*, *A. rufinus*.

HABITAT Grasslands, steppe, moorland, all types of savanna and derived grasslands within forest belts. In north-east Africa versatile *A. niloticus* ranges from sea level up to 2,000m, arid-adapted *A. neumanni* occurs between 400 and 1,500m. *A. abyssinicus* inhabits the rocky short-grass steppe and sedge bogs of northern Ethiopia (2,000–3,400m) while the late-rising, colonial-living *A. blicki* shelters in burrows with other species in afro-montane 'dega' habitat and in 'wurch' (afroalpine and subalpine moorlands).

FOOD Diurnal foragers on leaves, stems, shoots and seeds of grasses.

STATUS Periodically reaches plague proportions and can be a significant agricultural pest.



A. niloticus

Medium-sized herbivorous animals with highly distinctive fenestrated skulls, small heads, long backs and a little known and mainly non-African evolutionary history. However, *Pronolagus* and *Poelagus* did evolve (probably on the south-eastern side of the continent) from a common ancestor entering Africa sometime around 12 mya. The ancestor of *Bunolagus* (a species now on the brink of extinction) probably entered several million years later, while the earliest authenticated fossils of modern hares, *Lepus*, date from about 2.6 mya. As is so often the case, vestigial populations of ancient or rare animals and plants survive only in South Africa. South Africa's parks, reserves and estates include countless 'Ecological Elders', the Riverine Rabbit, *Bunolagus*, and red rock-hares, *Pronolagus*, among them. The greatest diversity of lagomorphs is still found at more temperate latitudes and altitudes.

True hares, of the family Leporidae, are medium-sized, soft-furred animals with short tails, relatively large ears, small mouths and forelegs that are shorter and slighter than the muscular hindlegs. All African hares and rabbits belong to this family. Teeth superficially resemble those of rodents in that the incisors are paired, chisel-like and well separated from the cheek-teeth. However, hare incisors are wholly sheathed in enamel, the upper pair backed by a second tiny incisor – 'peg teeth'.

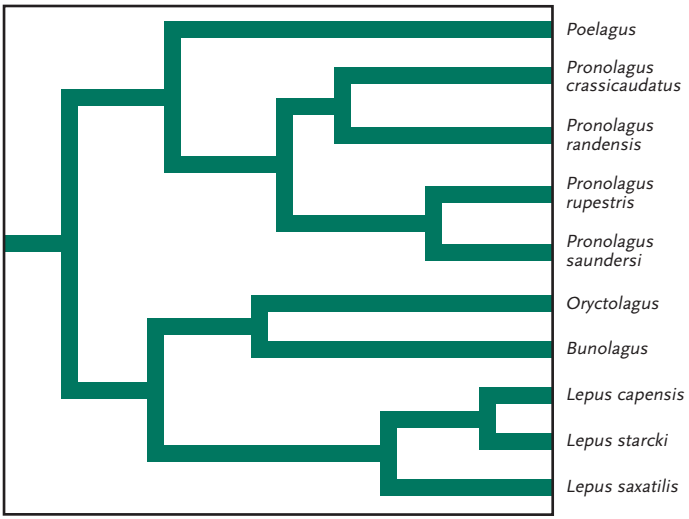
A wide scatter of rare relict hares in North America, Eurasia and Africa represent remnants of extensive past radiations. Red rock-hares, Bunyoro Rabbits and Riverine Rabbits are all, to a greater or lesser extent, African relictual groups. The single most successful and widespread genus, the true hare (*Lepus*), is the most recently evolved and is, possibly, partially displacing several earlier types.

Hares often flourish in exposed and unstable habitats and can endure repeated population booms and busts. They can survive on a coarse plant diet and their ability to extract nutrients is enhanced by recycling excreted pellets (called caecotrophs).

Distinctions between hares and rabbits are sometimes semantic but, as a rule, 'rabbits' live in burrows and have large litters of helpless young, while hares are solitary, live in the open and bear fewer, more precocious young. Various scent glands help regulate their social life. Anal glands scent dung (often deposited in piles). The activity of orbital glands is known to be linked with sex hormones, as is the penetrating odour of urine in males and activity of the male chin glands (both of which are used to mark objects and other animals). Inguinal, or groin, glands serve to produce a seasonal, sexual attractant.

Hares are visually alert but mainly depend on hearing and scent to detect predators. They have specialised fur which serves as an excellent insulator, kept dry and clean by shaking and frequent grooming. Fur is also moulted regularly. Populations exposed to extremes of heat (such as desert-dwelling hares) have very large, naked ears in which fine veins help cool the blood.

Profiles begin with more conservative species, ending with modern hares.



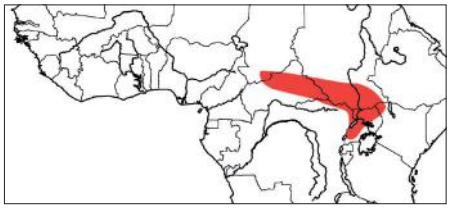
Tentative phylogenetic tree for the Lagomorpha (in part after Robinson and Matthy 2005).

HARES, ROCK-HARES AND RABBITS LEPORIDAE

Bunyoro Rabbit (Uganda Grass-hare)	*Poelagus marjorita*
Rock-hares	*Pronolagus* (3 species)
Common Rabbit	*Oryctolagus cuniculus*
Riverine Rabbit	*Bunolagus monticularis*
True hares	*Lepus* species

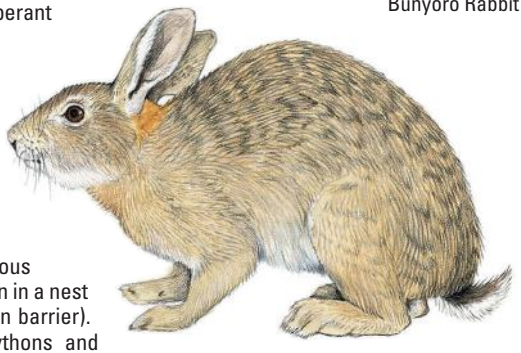
BUNYORO RABBIT

Poelagus marjorita



Bunyoro Rabbit

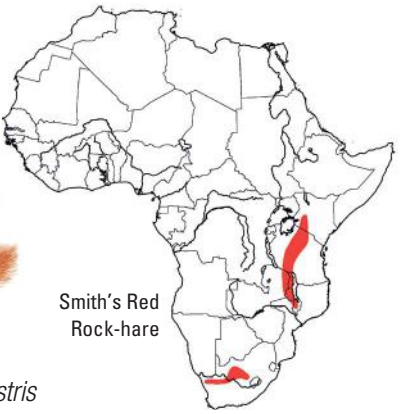
OTHER NAMES Uganda Grass-hare. Fr. *Lapin sauvage d'Afrique centrale*. Ger. *Bunyoro buschkanninchen*. Swah. *Sungura ya Bunyoro*.
MEASUREMENTS HB 400–605mm. T 38–70mm. W 2.2–3.1kg.
RECOGNITION Resembles the Common Rabbit but the fur is coarser, the nose more protuberant and the hindfeet proportionately shorter.
DISTRIBUTION Uganda to central Africa.
HABITAT Moist, wooded grasslands associated with rocky or broken ground. It shelters in dense vegetation, rock clefts and self-made 'scrapes'.
FOOD Grasses (preferably short), grass seeds, herbs and, occasionally, cultivated crops
BEHAVIOUR Bunyoro Rabbits are continuous breeders and the helpless young are born in a nest (blocked by the mother with a vegetation barrier). Predators include Servals, jackals, pythons and birds of prey. Mainly nocturnal and solitary or in very small groups.
ADAPTATIONS Dependent on abundant shelter from rocks, bushes or dense grass; they lack the stamina and speed of true hares. The muscles are pink (as in Common Rabbits) not red (as in hares).
STATUS Locally declining but unlikely to be threatened overall. Occurs in several national parks.



ROCK-HARES *Pronolagus*

Smith's Red Rock-hare	*Pronolagus rupestris*
Hewitt's Red Rock-hare	*Pronolagus saundersiae*
Natal Red Rock-hare	*Pronolagus crassicaudatus*
Jameson's Red Rock-hare	*Pronolagus randensis*

Chunky, grizzled hares with a red or dark tail, a grey head and reddish limbs. Very discontinuously distributed in southern Africa and the Eastern Rift Valley to Kenya. They inhabit broken and rocky country or areas with abundant cover of bushes and grass. Populations of rock-hares are scattered and patchy in distribution. They are primarily grazers. All species are closely associated with cooler climates and rocky habitats where agility over well-known broken ground pre-empts competition from true hares, *Lepus* spp., which are adapted to more open country. Solitary and nocturnal but occasionally also active by day. One or two young born in a helpless condition in plant- and fur-lined nests. Preyed upon by pythons, eagle-owls and Black Eagles. All species are well represented in reserves and national parks, but have been inadequately studied.



Smith's Red Rock-hare

SMITH'S RED ROCK-HARE *Pronolagus rupestris*

OTHER NAMES Fr. *Lièvre roux de Smith*. Ger. *Smith-Rothase*. Swah. *Sungura ya Mawe*.

MEASUREMENTS HB 380–535mm. T 50–115mm. W 1.30–2.05kg.

RECOGNITION Grey-headed hare with a bright russet rump and legs. The red tail normally has a black tip. The black colour is variable and the fur is soft and dense.

GEOGRAPHIC VARIATION East African population requires taxonomic investigation. Pelage colour varies geographically.

HABITAT Stony country where dense bush, grass and rocks are intermingled. Shelter in 'forms', like other hares, usually under slabs of stone or in crevices. They use habitual latrines where they are said to be readily trapped. Solitary animals, they will congregate temporarily on grassy lawns at night.

FOOD Mainly grazers.

STATUS Extremely discontinuous distribution and relatively small patches of suitable habitat may mean that local populations are vulnerable to extinction. IUCN rates as of least concern.

HEWITT'S RED ROCK-HARE

Pronolagus saundersiae

OTHER NAMES Fr. *Lièvre roux de Hewitt*. Ger. *Hewitts Rothase*.

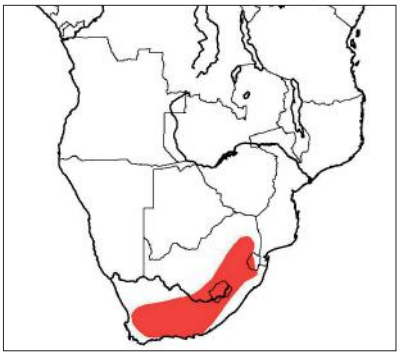
MEASUREMENTS HB: 380–535mm. T 50–115mm. W 1.35–2.05kg.

RECOGNITION Formerly described as a subspecies of *P. rupestris*, this population is now regarded as a distinct species. Distinguished by its relatively short ears, small head, rufous forelegs, pale-grey cheeks, brown throat-spot and fluffy, longish sandy or russet tail.

HABITAT Steep, rocky hillsides at generally higher elevations than other red rock-hare species. Dominant plant communities are *Protea* fynbos, *Buddleja/Leucosida* scrub and afroalpine *Erica/Helicrysum* heath.

FOOD Nocturnal grazer in highland grass–scrub mosaics.

STATUS Common in ecologically suitable habitat.



Hewitt's Red Rock-hare

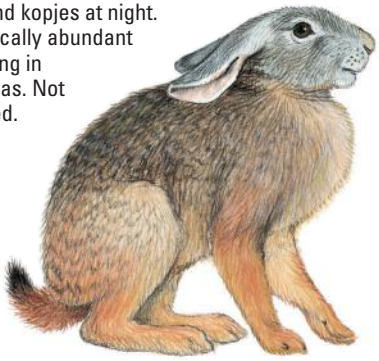
Natal Red Rock-hare

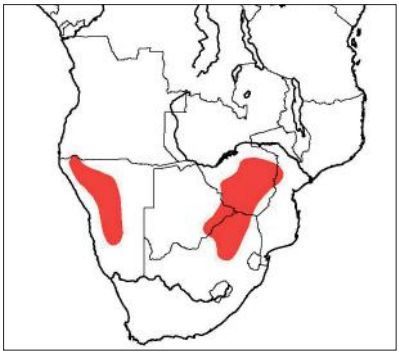
NATAL RED ROCK-HARE *Pronolagus crassicaudatus*

OTHER NAMES Fr. *Lièvre roux du Natal*. Ger. *Natal-Rothase*.
MEASUREMENTS HB 460–560mm. T 35–110mm. W 2.4–3.0kg.
RECOGNITION Rock-hare with a pale grey band across the cheek, russet fore- and hindlegs and rump, and an all-russet tail. The dense fur is harsher than in other rock-hares.
GEOGRAPHIC VARIATION Five subspecies sometimes listed.
HABITAT Steep, grassy hillsides with scattered rocks and boulders along the eastern seaboard of South Africa and S Mozambique from East London to the R. Maputo, and from sea level up to 1,550m. Shelters among the rocks in tussocks or dense, low vegetation.
FOOD Grasses are grazed at night. Animals often move to higher elevations to graze and may do so in close proximity to each other.
STATUS Locally abundant. Seasonally and nominally protected as 'game'.

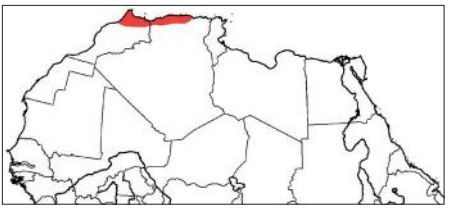
JAMESON'S RED ROCK-HARE *Pronolagus randensis*

OTHER NAMES Fr. *Lièvre roux de Jameson*. Ger. *Rand-Rothase*.
MEASUREMENTS HB 420–500mm. T 60–135mm. W 1.80–2.95kg.
RECOGNITION Rock-hare with a light-grey head with brownish flecks and a light, warm-coloured rump and back legs. The red-brown tail has a black tip. The fur is very soft and silky.
GEOGRAPHIC VARIATION *P. r. randensis* (Transvaal and Zimbabwe), *P. r. caucinus* (Namibia).
HABITAT Rocky hills, valleys and gorges in two widely separate areas of southern Africa (Zimbabwe–Transvaal and Namibia). They are very agile among boulders and able to run over very steep surfaces. They shelter among rocks and tussocks during the day.
FOOD Fresh green flushes of grasses are favoured and are usually grazed in proximity to rocks and kopjes at night.
STATUS Locally abundant but declining in settled areas. Not endangered.





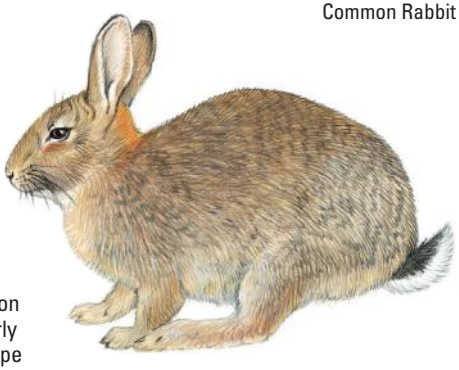
Jameson's Red Rock-hare



Common Rabbit

COMMON RABBIT

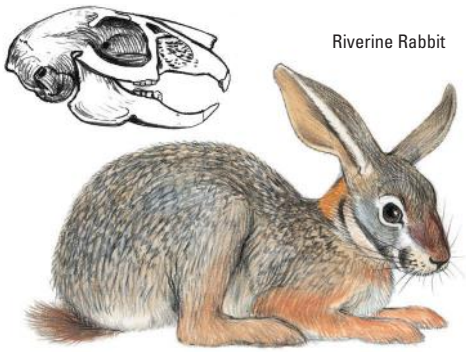
Oryctolagus cuniculus



OTHER NAMES Fr. *Lapin*. Ger. *Wildkaninchen*.
MEASUREMENTS HB 355–380mm. T 65–70mm. W 0.8–3.0kg.
RECOGNITION Small, short-limbed, brown-coated rabbit or 'digging hare', with shorter ears and a rounder head than true hares. The tips of the ears are never black.
GEOGRAPHIC VARIATION *O. cuniculus huxleyi* (S Spain, S France and N Africa): possibly original wild stock.
DISTRIBUTION It is uncertain whether the Common Rabbit was endemic to NW Africa or a very early introduction from Spain. Its spread into N Europe and transportation to Australia, South America and innumerable islands has been a result of human intervention.
HABITAT Bushy and broken country in N Morocco and NW Algeria, avoiding densely wooded land and desert. Rabbits live on the surface when predators and the climate allow. The digging of dens, burrows or warrens is likely to represent a response to a combination of environmental pressures.
FOOD Grass and herbs; bark in winter.
BEHAVIOUR As with all hares, Common Rabbits produce a variety of scents that help to regulate their social behaviour. Males mark out their home-ranges with pellets, urine and chin secretions. Increasing density and social clustering generally increase the animals' intolerance of the same sex (either generally or towards strange animals from outside their own 'family' group). They breed all year, are fertile by 4 months and can live for up to 8 years. Gestation lasts 1 month and the young, born blind and helpless in a burrow or nest, are weaned in 3 weeks. Their potential for increase is legendary and as many as 45 young can be born to a single female in 1 year.
ADAPTATIONS The Common Rabbit's fecundity has evolved to withstand very high levels of predation. Where predators have been destroyed, reduced or are absent (as in Europe, Australia and on islands), they accommodate to their own huge numbers by forming large 'family' groups in 'warrens', or burrow clusters, and defend their group territories against other groups. Where numbers are few and shelter is ubiquitous, Common Rabbits are spaced out more evenly, have less frequent aggressive encounters and show more resemblance to other hare species.
STATUS Common and intensively hunted in NW Africa, where it damages crops.

RIVERINE RABBIT *Bunolagus monticularis*

OTHER NAMES Fr. *Lièvre des buissons*. Ger. *Buschhase*.
MEASUREMENTS HB 337–470mm. T 70–108mm. W (est.) 1–2kg.
RECOGNITION A long-eared, medium-sized hare with relatively short hindfeet, a brown tail and a very conspicuous dark line separating the white chin and bib from the darker muzzle and cheeks. There are conspicuous pale eye-rings and white fringes along the upper edges of the ears.
DISTRIBUTION Restricted to a single river system in the central area of the Karoo plateau, Cape Province, South Africa.
HABITAT Dense vegetation bordering seasonal rivers in the Karoo where salt-loving plants, such as *Salsola* and *Lycium*, predominate. The Riverine Rabbit digs short burrows which it plugs with debris when not in use.
FOOD Browses on common shrubs, i.e. *Salsola*, *Kochia* and the ubiquitous *Mesembryanthemum*.



Riverine Rabbit

BEHAVIOUR Solitary, with male home-ranges of about 20ha and female, 13ha. Activity is nocturnal. Single young, weighing only 40g at birth, are reared in a fur- and grass-lined burrow.

ADAPTATIONS May represent a now ecologically specialised relict of a once more-widespread African hare, displaced, perhaps, by the arrival of *Lepus* from Eurasia.

STATUS Some 60% of Riverine Rabbit habitat has been destroyed for wheat cultivation and fragmented by farms. Nominally protected from hunting, but wild felids are known and effective predators. IUCN rates as critically endangered.

TRUE HARES *Lepus*

Cape Hare	*Lepus capensis* (includes *L. habessinicus, L. fagani*)
Scrub Hare	*Lepus saxatilis* (includes *L. victoriae, L. crawshayi*)
Starck's Hare	*Lepus starcki*

Typified by their long limbs and long ears, true hares have a short black-and-white tail. Body colour and face patterns vary greatly, notably between regional populations of the same species. Found over all grassy and subdesertic areas of Africa, where found in completely open country (Cape Hare), and grasslands with abundant cover (Scrub Hare). A third African species, Starck's Hare, is likely to represent a population of the European Hare, *L. europaeus*, that became stranded in Ethiopia after a glaciation and has subsequently adapted to the high-altitude moorlands.

Feed on grass, leaves, stems, seeds, herbs and bark. Different proportions of locally available plant parts are preferred by each species.

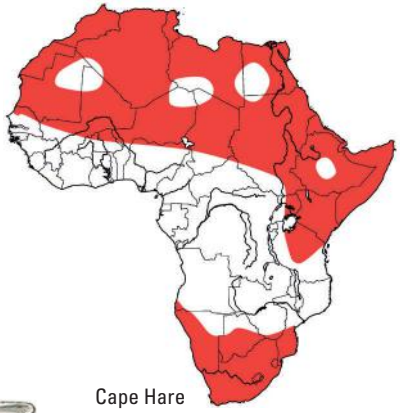
Hares are not known to be territorial but hierarchies form that include both sexes. Home-ranges are well known and regularly traversed along preferred trails. Sheltered sites for sunning, sleeping or sand-bathing are also regularly used. Home-ranges from 5 to many tens of hectares: densities fluctuate widely, with up to 10 animals per ha during boom periods.

Glandular scents help to regulate sexual and social behaviour. Scent, sound and movement provide important clues in detecting predators. Hares growl, grind their teeth and drum with their forelegs during aggressive or confident encounters. They scream when seized or wounded and females utter soft bleats when approaching their young. African hares breed continuously, females bearing about six litters a year, normally with one or two young per litter. Young born fully haired, eyes open, after 42 days' gestation. Lie up in concealed 'forms' but grow fast; fully mobile and independent by 1 month, sexually mature by 8 months. Oestrous females attract persistent male attention and frequent copulations.

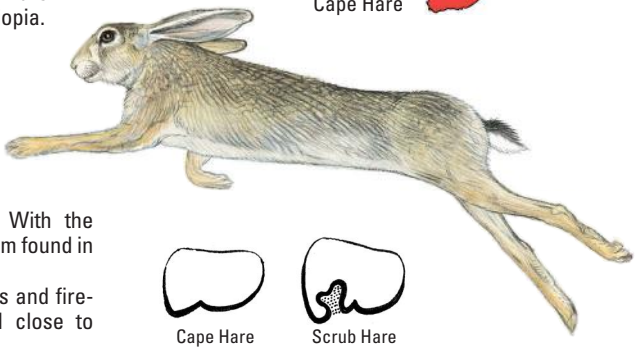
True hares have light skulls and skeletons, long backs and limbs, large hearts and lungs, red muscles and enlarged air passages, all of which represent adaptations for fast, manoeuvrable and sustained running (at up to 70km/h). In contrast to their 'last resort' strategy of fleeing, hares will crouch in total immobility until a potential predator approaches too closely. Their cryptic colouring and crouching are particularly important defences against birds of prey. However, predominantly nocturnal activity provides some protection against the latter.

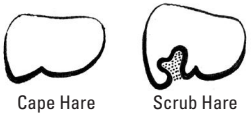
CAPE HARE *Lepus capensis* (includes *L. fagani* and *L. habessinicus*)

OTHER NAMES Fr. *Lièvre du Cap*. Ger. *Kap-Hase*. Swah. *Sungura*.
MEASUREMENTS HB 445–550mm. T 100–145mm. W 1.70–2.45kg.
RECOGNITION Back variable light shades of brown, buff or grey, chest normally sandy coloured. Muted contrasts on face and nape. Incisors without deep grooves, white forehead spot rare. Great regional variation.
GEOGRAPHIC VARIATION More than 30 subspecies have been named; included here is the small, desert-dwelling Abyssinian Hare *L. c. habessinicus* (Horn of Africa) and Ethiopian Hare *L. c. fagani* in highland north Ethiopia.
HABITAT Prefers completely open grasslands, steppes and subdesert. Cape Hares will move into cleared or regularly fired grasslands (only to be displaced by Scrub Hares if there is extensive woody regrowth). With the exception of *L. c. fagani*, seldom found in montane areas.
FOOD High proportion of herbs and fire-dependent grasses, cropped close to the ground.
STATUS Not endangered. Benefits from woodland clearance and overgrazing.



Cape Hare



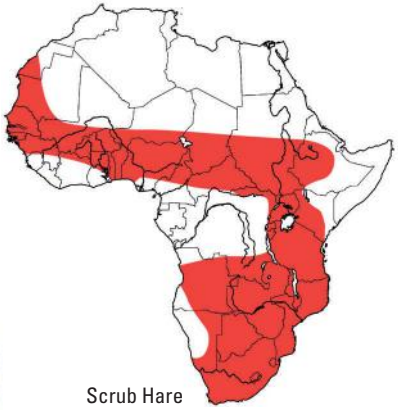


Cape Hare Scrub Hare

cross-section of incisor teeth

SCRUB HARE *Lepus saxatilis* (includes *L. victoriae* and *L. crawshayi*)

OTHER NAMES Fr. *Lièvre des buissons*. Ger. *Busch-Hase*.
MEASUREMENTS HB 415–768mm. T 68–175mm. W 1.5–4.5kg.

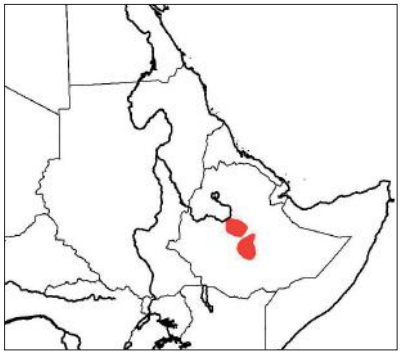


Scrub Hare

RECOGNITION Back variable, darker shades of brown to grey, with all-white underparts and well-defined pattern contrasts on the face. Nape of neck apricot to orange ochre; white forehead spot common. Deeply grooved incisors and muzzle projects more than in Cape Hare. Regional variation very substantial, notably in length of ears.
GEOGRAPHIC VARIATION More than 30 races have been named. Distinctive major populations (regarded as species by some authorities) are: Scrub Hare, *L. s. saxatilis* (southern Africa); *L. s. whytei* (SE Africa), *L. s. crawshayi* (central Africa), Savanna Hare, *L. s. victoriae* (East Africa), *L. s. ansorgei* (west-central Africa), *L. s. canopus* (West Africa).
HABITAT Prefers scrubby grasslands, grassy areas within woodlands, secondary growth, cultivation mosaics and stony, wooded steppes; common in upland and montane grasslands.
FOOD Rank grass species, which are cropped less close to the ground. In East Africa, Scrub Hares take fewer herbs than Cape Hares.
STATUS Not endangered.

STARCK'S HARE *Lepus starcki*

OTHER NAMES Ethiopian Highland Hare. Fr. *Lièvre éthiopien*. Ger. *Starck-hase*.
MEASUREMENTS HB (est.) 420–600mm. T 70–120mm. W 2.0–3.5kg.
RECOGNITION Back mottled tawny, becoming grey on the rump. Nape, sides, chest and legs tawny, underparts white. Tail all white or with black stripe. Prominent black tips to ears.
HABITAT High-altitude moorlands (2,500–4,000m) in Ethiopia.
FOOD Common moorland grasses (*Agrostis*, *Eleusine*, *Festuca*, *Pennisetum* and *Poa*) are likely food plants.
STATUS Common within a restricted habitat; is reported to fluctuate in numbers. (It may be an Ice-Age isolate of the European Hare, *L. europaeus*.) Probably not threatened at present.



Starck's Hare

The concept of a distinct order for hedgehogs was pioneered by that hugely perceptive evolutionary thinker and mentor, William King Gregory, in 1910. Hedgehogs (and their Asian relatives, the gymnures) derive from late Cretaceous mammals that also gave rise to shrews and bats.

The most striking adaptation of hedgehogs is their ability to curl up into a spiny ball. Correlated with this are short blunt ridges on the vertebrae and a wide pelvis, but the main modification is the hemispherical muscle in which the spines are embedded. When this muscle (which is anchored to the forehead) contracts it becomes a bag into which body, head and legs are withdrawn. The spines are an effective protection, although eagle-owls and some hungry carnivores show few difficulties in killing, 'debagging' and eating hedgehogs.

Primary senses are auditory and olfactory but the size of ear bullae and pinnae varies between species. Hedgehogs are also celebrated for their ability to lay down fat and become torpid during periods when foods are scarce and temperatures are hostile. They are omnivorous with a preference for well-protected prey such as beetles, centipedes, crabs, snakes and snails for which some resistance to toxins, and strong, sharp cusped teeth are useful adaptations.

Of 14 Old World species, six occur in Africa.

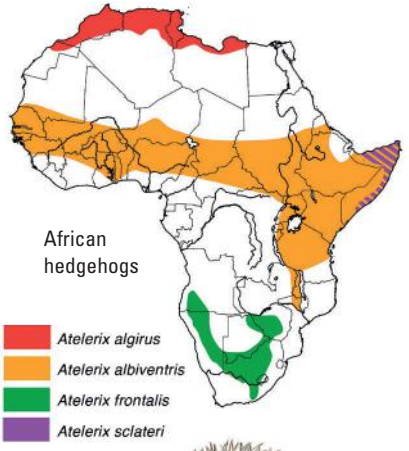
HEDGEHOGS ERINACEIDAE

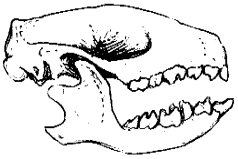
African hedgehogs	*Atelerix* (4 species)
Long-eared Hedgehog	*Hemiechinus auritus*
Desert Hedgehog	*Paraechinus aethiopicus*

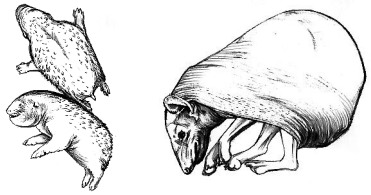
Hedgehogs are successful and widespread modern survivors of a very ancient group. The evolution of spiny armour has been a major factor in their survival. They have relatively short legs and tail, a sharply pointed face, small eyes and prominent ears. They are nocturnal insect-eaters.

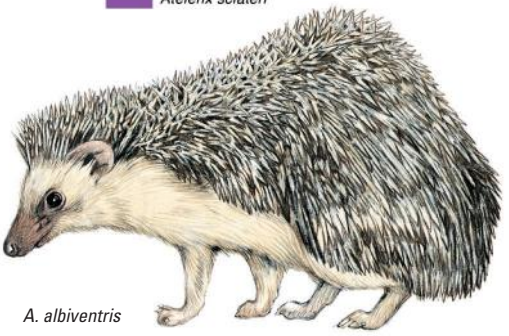
AFRICAN HEDGEHOGS *Atelerix*

OTHER NAMES Fr. *Hérissons*. Ger. *Igel*.
MEASUREMENTS HB 140–250mm. T 15–50mm. W 250–1,600g.
RECOGNITION Small, spiny animals with short tails, pointed muzzles and short hairy legs with clawed, well-padded toes. Only active in evenings or at night, they make a sniffing call. They trot with fast leg movements but hunch or roll into a prickly ball at any disturbance.




A. frontalis


newborn hedgehogs (*left*) and a hedgehog's muscular bag (*right*)

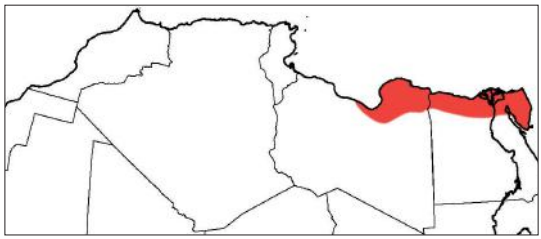

A. albiventris

SPECIES *A. albiventris* (sub-Saharan non-forest habitats to R. Zambezi), *A. algirus* (Libya to W Sahara), *A. frontalis* (southern Africa), *A. sclateri* (Somalia).
DISTRIBUTION Widespread but sporadic in drier regions of Africa.
HABITAT Marked preference for relatively open, dry or seasonal habitats with sparse or patchy grass cover, especially overgrazed regions with dense ungulate populations.
FOOD Invertebrates, notably termites, beetles, earthworms and millipedes, small vertebrates, fungi and fallen fruits. Can locate hidden prey by scent and sound, and can dig in soft, loose soils.
BEHAVIOUR Nocturnal or crepuscular, solitary except females with young. Hibernates in temperate regions: may also aestivate in tropical dry seasons. Vocalisations include sniffs, growls, twitters, spitting, chatters and screams. Travels over home-range, sleeping in changing (but sometimes habitual) day-shelters. One to nine young born seasonally.
STATUS Although some *Atelerix* species are considered rare, most are widely distributed. The Somali hedgehog (*A. sclateri*) is of uncertain taxonomic status and could be a subspecies of *A. albiventris*.

LONG-EARED HEDGEHOG

Hemiechinus auritus

OTHER NAMES Fr. *Hérisson a grandes oreilles*. Ger. *Langohr-igel (Grossohrige)*.
MEASUREMENTS HB 156–206mm. T 18–39mm. W (est.) 150–500g.
RECOGNITION A small and variably coloured hedgehog, but generally pale with shorter spines and larger ears than other African hedgehog species. Only active at night (or on overcast, cool mornings or evenings), they often sleep in rodent burrows during day. Females squeal in defence of their young and butt with their head spines.



Long-eared Hedgehog

HABITAT The eastern Mediterranean littoral. Has a limited range in Africa, being a mainly Asiatic species. *H. auritus* is a moisture-dependent hibernator preferring cool deserts.
FOOD Mainly invertebrates, notably insects and millipedes. Snails favoured in spring.
STATUS Not endangered.

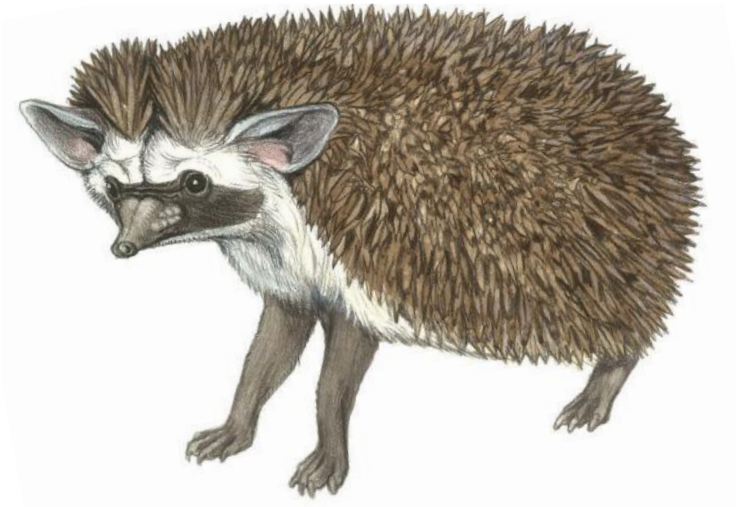
DESERT HEDGEHOG

Paraechinus aethiopicus

Desert Hedgehog

OTHER NAMES Ethiopian Hedgehog. Fr. *Hérisson du désert*. Ger. *Wustenigel*.
MEASUREMENTS HB 169–217mm. T 15–22mm. W (est.) 500g.
RECOGNITION Variably coloured desert hedgehog with two distinctive 'coronets' of spines on either side of a narrow spineless peak to the broad white forehead. Anterior tooth-row more gracile than in other species and the external muzzle therefore visibly finer and sharper than in other African hedgehog species. Ears shorter than in *Hemiechinus*, longer than in *Atelerix*. Fast and long-legged, carrying its body well clear of the ground.

Has physiological adaptations to minimise water-loss and increase metabolic efficiency. Sleeps in self-dug burrows or in natural retreats under vegetation or among rocks during the day.
HABITAT Deserts. Aestivates in hot, dry hamadas as well as mountains of the Sahara desert. Prey to owls and jackals.
FOOD Invertebrates and vertebrates such as small reptiles.
STATUS Not endangered.



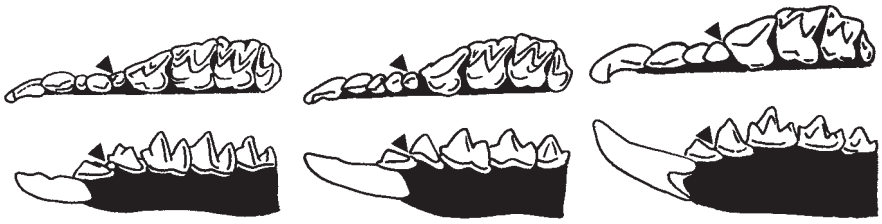
SHREWS SORICOMORPHA

Evidence for the exceptional evolutionary insights of W. K. Gregory lies in his recognition, in 1910, that shrews constituted a unique order of mammals. Recent genetic analyses suggest that the ancestral shrews probably shared late Cretaceous origins with hedgehogs and bats. Shrews are thought to have first entered Africa, from Eurasia, about 18 mya.

SHREWS SORICIDAE

Mouse shrews	*Myosorex* (14 species)
Mole shrews	*Surdisorex* (2 species)
Congo shrews	*Congosorex* (3 species)
Musk shrews	*Suncus* (9 species)
Forest shrews	*Sylvisorex* (12 species)
Hero shrews	*Scutisorex* (2 species)
Rwenzori Shrew	*Ruwenzorisorex suncoides*
Rodent shrews	*Paracrocidura* (3 species)
White-toothed shrews	*Crocidura* (105 species)

Shrews are small, mouse-sized mammals with a long, mobile nose and a stout, cylindrical skull. Adapted to bulldoze insects out of their retreats in plant debris: to this end their bodies are powerful and tubular. Sensitive vibrissae monitor surroundings and detect prey. Incisors function as pincers and molars as shredders of hard insect chitin. A very ancient group with recognisable fossil ancestors dating back more than 40 million years in Eurasia but first shrew fossils in Africa are from between 18 and 15 mya.



$\frac{3—1—2—3}{2—1—1—3} = 32$

tooth formula

Myosorex

$\frac{3—1—2—3}{2—0—1—3} = 30$

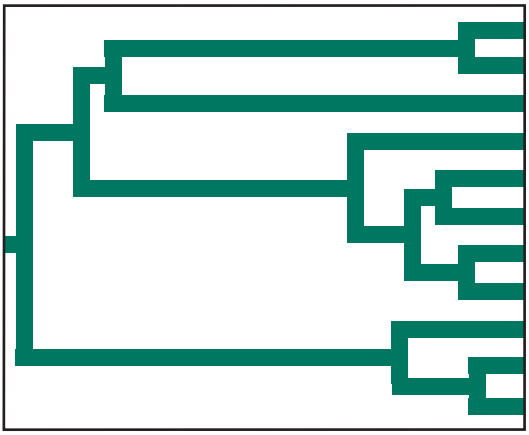
tooth formula

Sylvisorex, *Scutisorex* and *Suncus*

$\frac{3—1—1—3}{2—0—1—3} = 28$

tooth formula

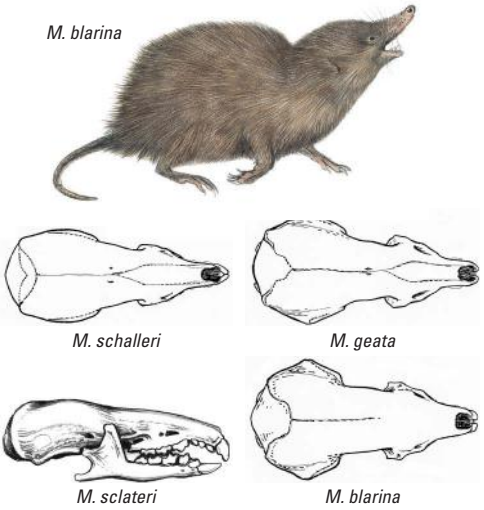
Crocidura and *Paracrocidura*

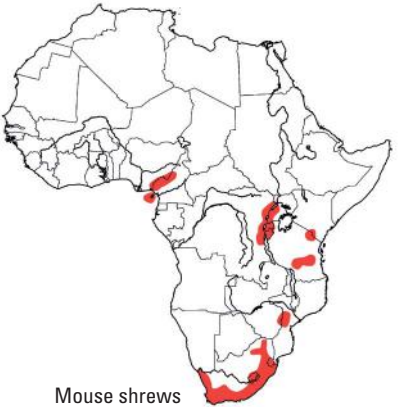


Tentative phylogenetic tree for the Soricomorpha (in part after Willows-Monro & Matthee 2011).

During evolution of shrews there has been progressive reduction of back molars and premolars. Nine African genera represent different phylogenetic levels, with *Myosorex* (with 32 teeth) the most ancient and *Crocidura* (28 teeth) the most advanced. The former, and its allies, are specialised or relict groups surviving in special habitats or ecological niches. *Crocidura*, with more than 100 species, is a highly successful advanced group.

Found in most habitats, they prefer moist conditions. Some are good climbers; others burrow underground. Scent glands on flanks probably assist in spacing individuals as well as repelling rival shrews. Also some secretions might repel predators. Most species are solitary except while breeding; all are highly aggressive to other shrews. Main predators are birds and snakes.



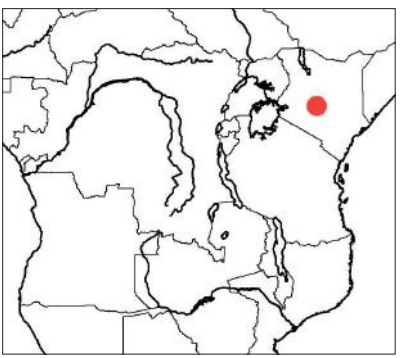

Mouse shrews

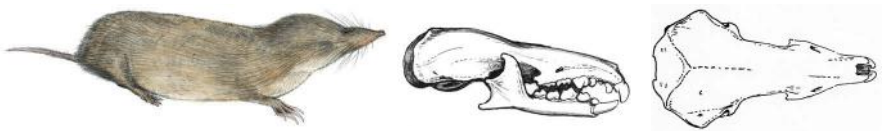
MOUSE SHREWS *Myosorex*

MEASUREMENTS HB (avg) 50–100mm. W 7.6–18g.
RECOGNITION Small, dark shrews, with reduced eyes and ears, a short tail and well-clawed, slender toes. Lower canines vestigial but upper ones retained. The last molars are well developed in both jaws, although smaller than the other two forward ones. (Dental formula: 3-1-2-3:2-1-1-3 = 32.)
SPECIES *M. babaulti*, *M. blarina*, *M. cafer*, *M. eisentrauti*, *M. geata*, *M. kihaulei*, *M. longicaudatus*, *M. okuensis*, *M. rumpii*, *M. schalleri*, *M. sclateri*, *M. tenuis*, *M. varius*, *M. zinki*.
HABITAT Mostly temperate or high-altitude regions, often in swampy conditions. Most species are highly localised endemics, relict descendants of once more widespread populations.
FOOD Small invertebrates, mainly insects and earthworms and some very small vertebrates (notably frogs).
STATUS Several species are described from one or a very few specimens. All are very poorly known.

MOLE SHREWS *Surdisorex*

MEASUREMENTS HB 82–110mm. T 20–35mm. W 16.0–27.5g.
RECOGNITION Small brown shrews with dense, short fur and no trace of external eyes or ears. The forelegs have long, sharp claws on robust digits but with slender palms and wrists (indicating relatively recent modification).

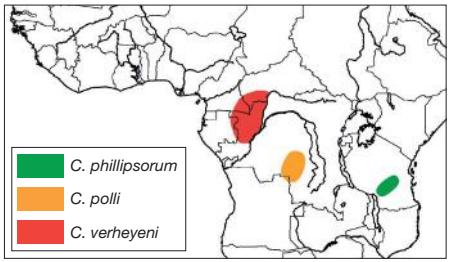

Mole shrews



S. polulus

SPECIES *S. norae* (Aberdare Mts), *S. polulus* (Mt Kenya).
HABITAT Surface runways and subterranean tunnels in afroalpine and upper montane forest zones; commonest in bamboo and grassland/sedge areas.
FOOD Mainly earthworms (intestines not eaten) and other invertebrates 'harvested' in tunnels and runways.
STATUS Not endangered.

C. polli



Congo shrews

CONGO SHREWS *Congosorex*

C. verheyeni

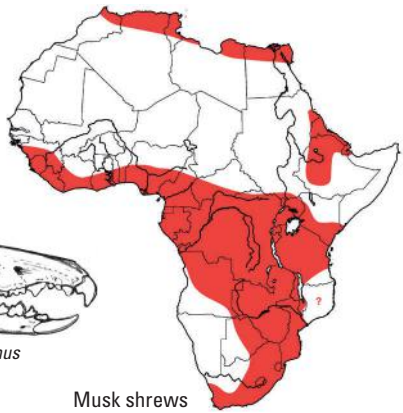
MEASUREMENTS HB 53–95mm. T 19–40mm. W 4–12g.
RECOGNITION Small brown shrews with longish tail and large ears (hidden in long fur in *C. phillipsorum*). Lack lower canines but otherwise skull resembles those of mouse shrews.
SPECIES *C. phillipsorum*, *C. polli*, *C. verheyeni*.
HABITAT Each species only known from a very limited area. *C. phillipsorum* from montane forest in the Udzungwa Mts. *C. polli* from Kasai, S DR Congo (presumed degraded forest galleries traversing fire-climax Miombo (*Brachystegia*) woodlands. *C. verheyeni* from rainforest in Congo/CAR.
FOOD Invertebrates.
STATUS Little known.

MUSK SHREWS *Suncus*

OTHER NAMES Dwarf shrews
MEASUREMENTS HB 40–81mm. T 25–97mm. W 1.5–8.0g.
RECOGNITION Very small shrews of various shades of brown or grey, with a paler underside. They have large rounded ears, a bewhiskered pink muzzle, thin limbs and a tapered tail. (Dental formula 3-1-2-3:2-0-1-3 = 30.) First African fossils about 8 mya.

S. varilla

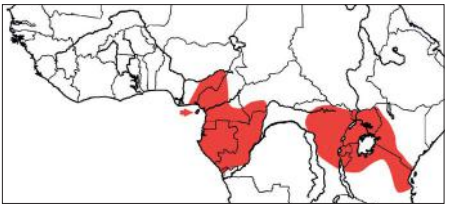
S. murinus



Musk shrews

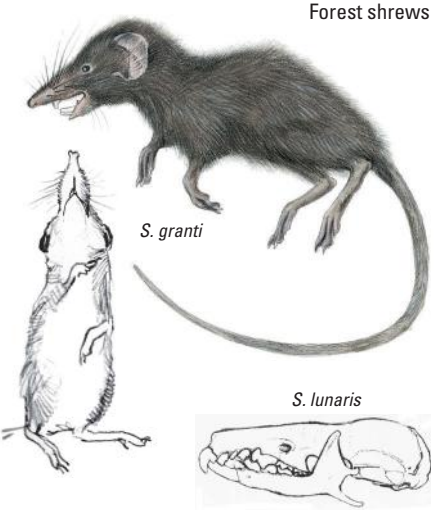
SPECIES *S. aequatorialis*, *S. etruscus*, *S. hututsi*, *S. infinitessimus*, *S. lixus*, *S. megalura*, *S. murinus*, *S. remyi*, *S. varilla*. (*S. murinus* introduced.)
HABITAT Very patchy distributions. Commonest in temperate regions but tropical *S. megalura* is a highly successful and widespread forest and woodland climber with long prehensile tail. Some species associated with termitaries.
FOOD Insects (up to shrew size) and other small invertebrates.
STATUS Unknown (inconspicuous and rarely trapped).

FOREST SHREWS *Sylvisorex*



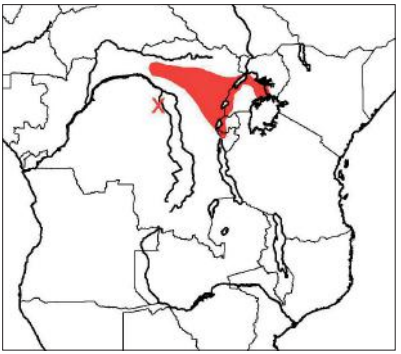
Forest shrews

MEASUREMENTS HB 43–93mm. T 26–61mm. W 2.3–20g.
RECOGNITION (Dental formula 3-1-2-3:2-0-1-3 = 30.) Dark brown or black shrews with extended noses, long tails and mobile digits on the hands and feet. Once thought to occupy a special arboreal niche, further study suggests that the arboreality of one or two species has had too much emphasis. Instead, *Sylvisorex* lacks an easily definable niche, variously resembling *Suncus*, *Scutisorex* and *Crocidura*, in a mosaic of micro-features that point to it having a broadly antecedent status, like *Myosorex*, with which it also shares characteristics. Ancestral features often co-exist with specialisation for difficult niches (i.e. *Myosorex* and *Surdisorex* resemble incipient moles) yet a majority of *Sylvisorex* species inhabit three refugial mountains without any glaringly obvious specialisation. When compared with the entire spectrum of African shrews at least one specialisation emerges for the majority of *Sylvisorex* species: a tolerance (probably physiological) for permanently wet and frequently cold habitats.
SPECIES *S. camerunensis*, *S. granti*, *S. howelli*, *S. isabellae*, *S. johnstoni*, *S. konganensis*, *S. lunaris*, *S. morio*, *S. ollula*, *S. oriundus*, *S. pluvialis*, *S. vulcanorum*.



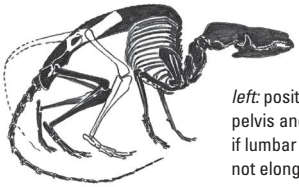
HABITAT Tropical shrews living in wet or riverine habitats from sea level up to 4,000m. Some species (notably *S. lunaris*) span multiple vegetation types at all altitudes. Some species (notably *S. granti* and *S. johnstoni*) appear to have widely discontinuous distributions. Others are extremely localised.
FOOD Invertebrates.
STATUS Little known. RNA of the deadly Ebola virus has been identified in *S. ollula* – another incentive to pursue further research on *Sylvisorex* shrews.

HERO SHREWS *Scutisorex*



Hero shrews

OTHER NAMES Armoured shrews.
MEASUREMENTS HB 105–150mm. T 70–109mm. W 70–113g.
RECOGNITION Very large grey shrews with long, tapered nose, shallow ears and dense woolly fur, thick with projecting guard hairs. Readily distinguished by a 'trotting' (rather than 'crawling') gait under an extraordinary hunched posture. The name derives from their use as warrior talismans



left: position of the pelvis and hind legs if lumbar region was not elongated

S. somereni

in N DR Congo. Mangbetu tribesmen first drew the attention of scientists to these species, asserting that 'not any kind of an attack can seriously injure them, much less bear them down'. A warrior then demonstrated that a hero shrew could bear the weight of a man by standing on it. That Mangbetu insight dramatised the fact that a lumbar fender, thickened skull and defensive posture effectively protected vital organs such as heart and brain. One evolutionary implication is that the shrew has a body built to anticipate attack. A second supposes that a significant number of predators must desist before killing the shrew. The most likely prediction to emerge is that these shrews possess some form of deterrent chemistry (irritant secretions? poisonous bite?) which serves to repel predators.

To evolve such defences, *Scutisorex* has doubled the number of lumbar vertebrae. Evolutionarily, it has achieved this by progressively sliding its pelvis down the spine. The vertebrae of the lower back have been elaborated into components of a complex shield or buffer-like structure by broadening, thickening and developing interlocking spicules along their outer margins. The laterally inflexible lower back and displaced pelvis contrasts with doubling-up of the forequarters into an S-shaped bend, which gives the shrew its peculiar posture. The body is carried well clear of the ground on long limbs, with fingers and toes that can splay widely.

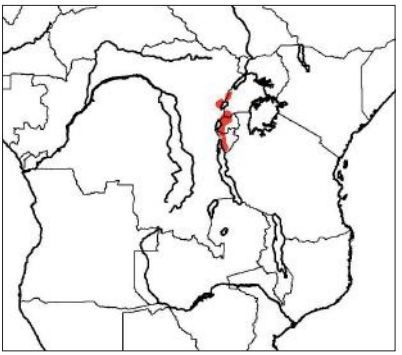
Adult animals, especially males, exude a very pungent scent and greasy yellow stains are visible on the sides and chest (perhaps secretions with a deterrent effect are involved?). They lay down substantial seasonal deposits of fat which alter the animal's appearance (fat animals seeming almost spherical in certain postures).

SPECIES *S. somereni*, *S. thori*. (*S. thori* is a newly discovered species from near Kisangani.)
HABITAT Seasonally swampy forests between the R. Itimbiri, R. Lualaba and R. Nile; found only at low and medium altitudes.
FOOD Invertebrates (caterpillars, earthworms, molluscs and grasshoppers) and small vertebrates (frogs). *Scutisorex* can swim and climb but finds most food on the forest floor. Prey appears to be immobilised by non-lethal bites, possibly due to toxins in the saliva.
STATUS Not endangered.

RWENZORI WATER SHREW *Ruwenzorisorex suncoides*

MEASUREMENTS HB 84–102mm. T 55–70mm. W (est.) 18–23g.
RECOGNITION A greyish-black shrew with a rounded head, short snout, armed with multiple vibrissae, and greatly reduced (but protruding) ears. It has short, small-toed pale forefeet and short, black hindfeet with blunt pale toes, presumably adapted for paddling, swimming and maintaining a grip in

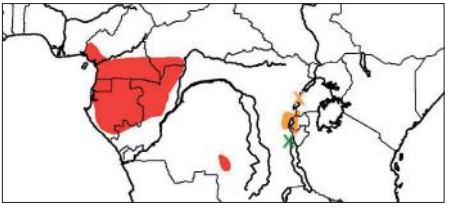
rushing water. The fur is dense, velvety and waterproof. Shortish tail, noticeably tapered.
HABITAT Lives beside montane forest streams in central Africa (E DR Congo, Rwanda, Burundi and W Uganda).
FOOD Aquatic invertebrates.
STATUS Uncontrolled illegal Coltan mining in its streams heightens concern for this species and other unique endemic biota.



Rwenzori Water Shrew

P. schoutedeni

incisors



P. schoutedeni
P. maxima
P. graueri

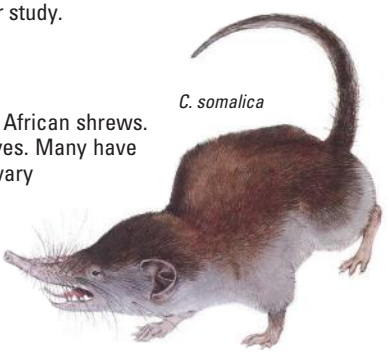
Rodent shrews

RODENT SHREWS *Paracrocidura*

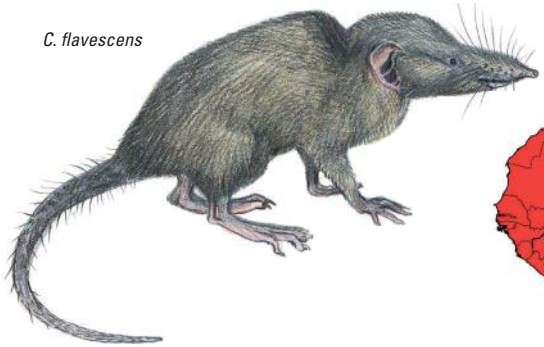
OTHER NAMES Large-headed shrews.
MEASUREMENTS HB 65–97mm. T 33–48mm. W 7–21g.
RECOGNITION Dark shrews with thin, short fur, dark skin and a short, broad muzzle. The shortish ears are nearly naked and are not hidden in the surrounding fur. Limbs are short, with minuscule claws, while the tail is shortish and finely haired. The upper incisors are laterally flattened to form cutting edges similar to those of rodents. Powerful jaw muscles in a large head imply forceful biting: this is more likely to be directed at gaining access to invertebrate prey than to the prey itself. Further research on this question is needed. Unusual in females (of *P. maxima*) having only two nipples, matched by litters of one or two young. This implies some measure of immunity from predation – still more research needed.
SPECIES *P. graueri*, *P. maxima*, *P. schoutedeni*.
HABITAT Montane and lowland forests from Cameroon to Uganda.
FOOD Invertebrates.
STATUS Locally common, so an inviting subject for further study.

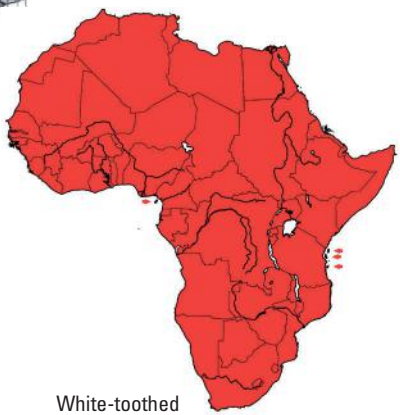
WHITE-TOOTHED SHREWS *Crocidura*

MEASUREMENTS HB 45–140mm. T 45–90mm. W 11–40g.
RECOGNITION The commonest and most diverse group of African shrews. All have a long, whiskery nose, visible ears and small eyes. Many have long, fine hairs growing sparsely on the tail but species vary in the extent of this pilosity.
SPECIES The more than a hundred species continue to daunt specialists and naturalists alike. Nonetheless, students of this shrew genus continue attempting to cluster species into supposedly related groups and sub-groups. Professor Heim de Balsac was the first to



C. somalica


C. flavescens


White-toothed shrews

divide *Crocidura* into three subdivisions on the basis of tooth reduction (especially of the last molar). One was 'conservative', another 'advanced' while the rest were 'mixed' (intermediate or indeterminate), the small selection illustrated follows this threefold grouping.

More recent molecular studies have confirmed that two identifiable clusters of species (the *turba/luna/fumosa* and the *bottegi/nana* groups retain karyotypes close to a putative ancestral type. Most *Crocidura* have, instead, multiplied the number of their chromosomes, suggesting a very substantial intra-African radiation. By contrast, non-African *Crocidura* (and more recent shrew immigrants to Africa) have been more typical in reducing the number of their chromosomes.

The study of this genus is a work in progress so the subgroups listed here must be regarded as tentative and provisional. They attest to the fact that *Crocidura* shrews, no less than other speciose biota, occupy a broad range of biogeographic regions in Africa and have diverged to fill numerous micro-niches.

The conservative *turba/luna/fumosa* group consists of: *C. turba*, *C. luna*, *C. fumosa*, *C. montis*, *C. selina*, *C. raineyi*, *C. grandiceps*, *C. taretta*, *C. zimmeri*.

The mainly montane complex of small, dark, dentally conservative shrews (see dental chart below) is the *monax/littoralis* group: *C. monax*, *C. littoralis*, *C. maurisca*, *C. grassei*, *C. stenocephala*, *C. lanosa*, *C. usambarae*, *C. kivuana*, *C. latona*, *C. ultima*, *C. congobelgica*, *C. desperata*, *C. eisentrauti*, *C. manengubae*.

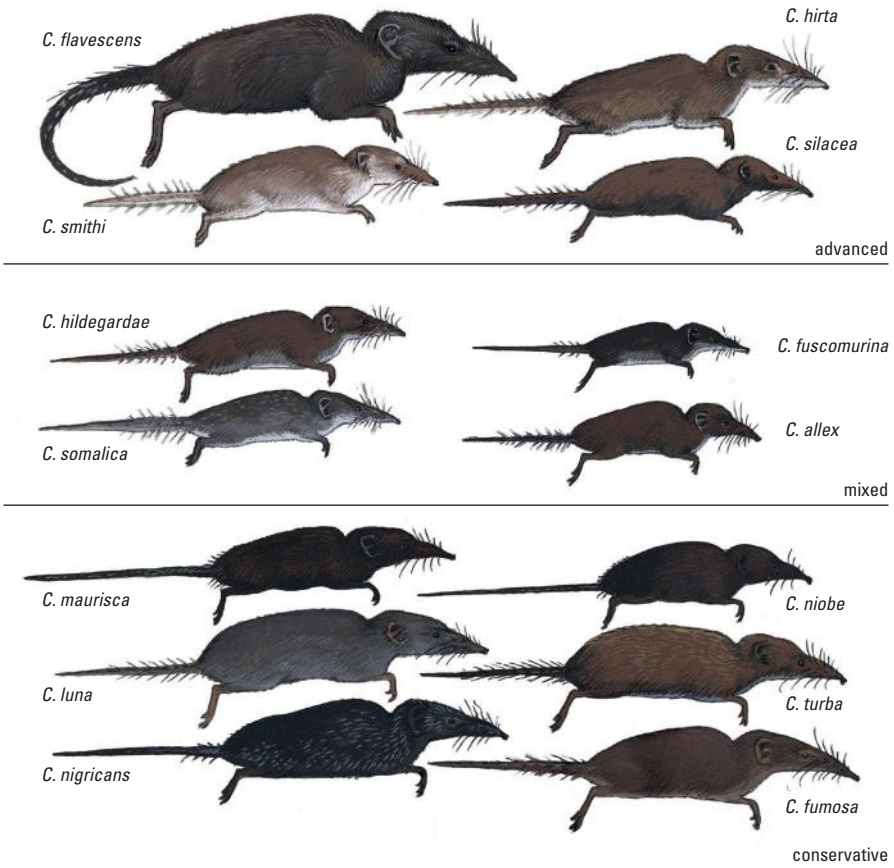
The *bottegi/nana* group consists of: *C. bottegi*, *C. bottegoides*, *C. nana*, *C. nanilla*, *C. lusitania*, *C. obscurior*, *C. pasha*, *C. religiosa*, *C. allex*.

A mainly forest-dwelling group, possibly allied, but more remotely, to the *turba* group is the *poensis* group: *C. poensis*, *C. foxi*, *C. theresae*, *C. nimbae*, *C. batesi*, *C. wimmeri*, *C. nigeriae*, *C. attila*, *C. mariquensis*, *C. buetikoferi*.

The 'mixed' *russula* group has affinities with Eurasian shrews: *C. russula*, *C. aleksandrisi*, *C. whittakeri*, *C. cinderella*, *C. tarfayensis*, *C. roosevelti*. Another cluster with a Eurasian link (resembling *C. suavolens*) is the very small-sized and successful *fuscomurina* group: *C. fuscomurina*, *C. elgonius*, *C. pitmani*, *C. maquassiensis*, *C. planiceps* (see dental chart below).

A widespread but even less certain grouping can be called the *hildegardae* and *dolichura* groups: *C. hildegardae*, *C. niobe*, *C. harenna*, *C. phaera*, *C. macowi*, *C. dolichura*, *C. jouventae*, *C. crossei*, *C. glacilipes*, *C. cyanea*, *C. crenata*, *C. douceti*, *C. muricauda*, *C. polia*, *C. denti*, *C. jacksoni*, *C. virgata*, *C. floweri*, *C. ludia*, *C. silacea*.

Half-palates for conservative (*left*), mixed (*middle*) and advanced (*right*) *Crocidura* spp.



Some *Crocidura* species. Coloration, relative body and hind-leg proportions, and tail pilosity.

The *hirta* group is a wide-ranging, 'advanced' and successful group of medium-sized shrews with long, narrow muzzles (see figures): *C. hirta*, *C. erica*, *C. greenwoodi*, *C. xantippe*, *C. nigrican*s. Closely related, but readily distinguished from the *hirta* group by their size, which is exceptionally large for a shrew, is the *flavescens* group (see dental chart opposite; note, some less closely related than others): *C. flavescens*, *C. olivieri*, *C. goliath*, *C. picea*, *C. mutesae*, *C. viaria*, *C. longipes*, *C. suahelae*, *C. zaphiri*, *C. fulvastra*, *C. telfordi*, *C. tansaniana*.

The *smithi* group tend towards prominent ears and a preference for dry habitats: *C. smithi*, *C. macartheri*, *C. fischeri*, *C. lamottei*, *C. voi*.

The *somalica* group ranges mainly north of the Equator: *C. somalica* (see p.319), *C. yankariensis*, *C. caliginea*. (*Paracrocidura* shrews might share ancestry with members of this group.)

C. ansellorum is a species difficult to assign to any current grouping. Likewise *C. parvipes* is a distinctive species that has been allocated to a subgenus *Afrosorex*.

HABITAT All vegetation types at all altitudes, mainly terrestrial, but able to climb and swim. Some species are highly restricted (particularly those in 'primitive', 'conservative' or specialised categories); others range very widely (notably some of the 'advanced' groups).

FOOD A very diverse range of invertebrates and small vertebrates.

STATUS The status of species that have been identified by IUCN as being of conservation concern are listed in *Mammals of Africa* (see Volume IV).

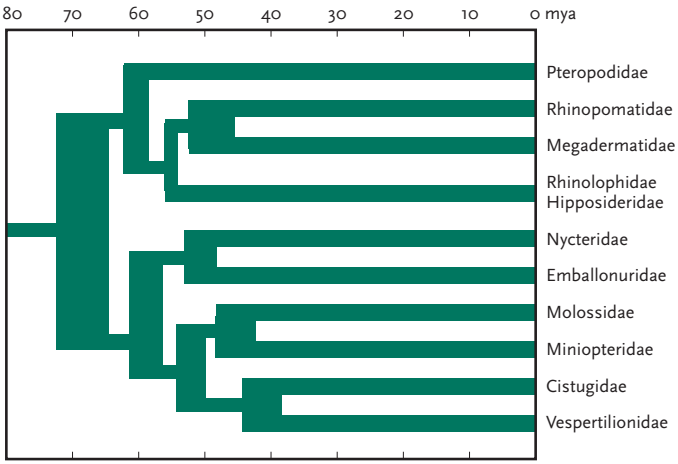
BATS CHIROPTERA

Fruit bats	Pteropodidae
Mouse-tailed bats	Rhinopomatidae
Large-winged bats	Megadermatidae
Horseshoe bats	Rhinolophidae
Leaf-nosed bats	Hipposideridae
Slit-faced bats	Nycteridae
Sheath-tailed bats	Emballonuridae
Pimple-winged bats	Cistugidae
Vesper bats	Vespertilionidae
Long-fingered bats	Miniopteridae
Free-tailed bats	Molossidae

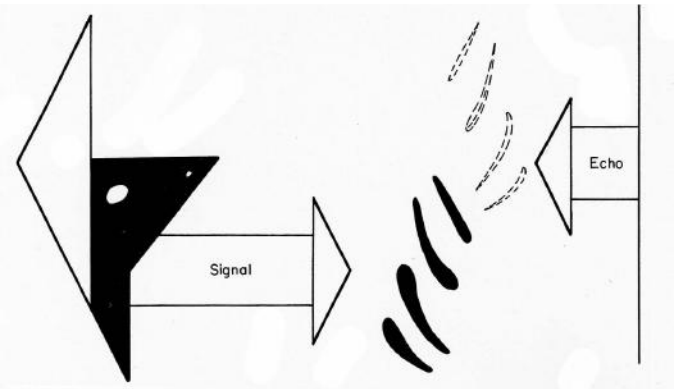
Modern genetics has finally settled years of speculation about the relationship between insect-eating bats and fruit bats with a surprising conclusion. The so-called 'insect bats' comprise two clusters, one of which is closer to fruit bats than it is to other insect-eating bats! While this guide still begins by profiling fruit bats, they are no longer treated at the high level of suborder. Instead they are the first of 11 bat families.

The range of forms and global distribution is greater than any other order of mammals, a diversity that relates both to the mobility and the early radiation of bats. Forearm lengths (the conventional measure of relative size in bats) range from 26mm to 163mm. Tooth numbers vary between 26 and 38. Each family represents a different mosaic of conservative and derived characteristics; thus mouse-tailed bats and some fruit bats have relatively 'primitive' wing bones and very evolved (long and thin) hindlimbs whereas the free-tailed bats have 'primitive' muscular legs and very advanced, high-performance wings.

For arboreal woodland insectivores the primary incentive to launch their small bodies into 'flying leaps' was likely to have combined the pursuit of prey and the need to reach other trees. The more fragmented of woodland canopies (especially those in very windy regions) would have posed the severest challenges and would have favoured animals with greater control over their glide. It may have been under these sorts of conditions (most probably in Asia) that the common bat ancestor evolved powered flight. Some bats catch prey in their 'hands', or rather in the membranes stretching from or between their fingers and tails, before a quick transfer to the mouth. This was possibly a capture technique among the early bats, which fossils indicate had already diversified into at least four lineages by 50 mya. Contemporary estimates of the age of the bat lineage range from about 88 to 64 mya.



Tentative phylogenetic tree for African bats (partly after Eick *et al.* 2005).



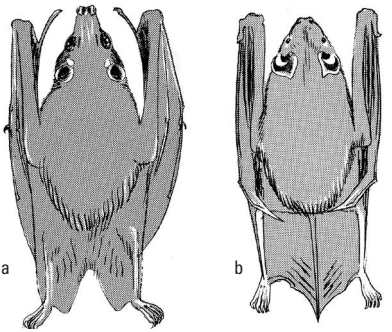
Schematic diagram of transmission and reception of bat echolocation.

Bats have used ultrasound to develop miniaturised forms of echo-location that are still infinitely superior to those devised by space or aeronautical engineers. Scientists, using bat-detecting equipment and ultrasound analysers, have begun to identify and classify bats according to their ultrasound signatures. Some of the most sophisticated echo-locators, such as the horseshoe bats, are already clearly recognisable in fossils dating back about 40 million years, which indicates that differentiation of specialised hunting techniques began very early on.

Bats have a world-wide distribution and many species (especially vesper bats) are able to hibernate, thus benefiting from the rich seasonal insect fauna of cool temperate regions. Some species are known to be nomadic or to migrate (a major feature of bat biology in Africa but in urgent need of further study). Such movements should be important indicators of seasonality in Africa and most movements are thought to occur within the continent. Long-fingered bats are known migrants and others, such as free-tailed bats, are also strong, long-distance fliers. Some bats, such as the strictly forest-dwelling horseshoe and leaf-nosed species, appear to have diverged many millions of years ago but species separated by many thousands of kilometres, even oceans and deserts apart, resemble each other because they are conservative species occupying relatively stable ecological niches and not because of recent migratory contact. Several groups have relatives as far afield as southern Asia and Australia, some of recent, some of ancient connection.

It might be expected that a majority of bats, being so mobile, would be ubiquitous or very widespread. This is true for some species but a majority have ranges that seem to be almost as biogeographically constrained as terrestrial mammals. Notably, occupation of the south–east and centre–west biogeographic realms apply for some bat genera no less than for terrestrial mammals. Current authorities have identified clusters, or species-groups, with geographic limits that broadly correspond with these evolutionary realms. Such groupings have provided some sequences for species lists and groupings in this guide.

Only the barest outlines of bat ecology are known. They inhabit all major terrestrial habitats from desert to moist rainforest. Many species are exclusively equatorial and do not tolerate cold. Some of these are effectively limited to sea-level altitudes. Others tolerate cold montane environments. The shelters that bats exploit are very varied and range from individual roosts in vegetation or in crevices to mass roosts in caves or mines. Some species space themselves while roosting, others hang in clusters, yet others pack together in tight wedges. As they are reluctant to fly during the day, most bats are best observed (discreetly) while at rest in their day-roosts.



(a) Fruit bat. Large eyes, second claw on wings and funnel-shaped ears. (b) Insect bat. Clawless wing, complex ears and teeth.

Invertebrates of various kinds (mostly insects) are caught by a variety of different techniques in different species (a bat's type of echo-location being a central aspect of its technique). Some catch fast-flying insects, others catch slow, fluttering ones, while others pluck invertebrates from vegetation or off the ground. Many species forage down valley or shoreline flyways and a few are known to ambush their prey from habitually used vantage points, like nocturnal flycatchers.

Bat societies include many permutations of aggregation: nursery groups; age groups; all-male, all-female and mixed crowds; stable pairs; and solitary mothers with offspring. Most species have pungent glands that fluctuate in size and appear to play a role in reproductive behaviour in most instances. Some species smear their roost with scent but most spread it by rubbing or scratching themselves.

Courtship may involve ritualised postures, flights, chases accompanied by special calls and the production and laying of scent trails. Copulation takes place in the roost or on a perch, with diverse embraces. Births are often very seasonal and the young may be carried continuously or 'parked' in nurseries or on their own. They mature very rapidly, nourished by a rich, concentrated milk; lactation can last 1–3 months. Bats employ various strategies to time births: these include sperm storage, delayed ovulation, delayed fertilisation and delayed implantation of an arrested 'foetus', or blastocyst.

Many bat species live for a long time (more than 25 years has been recorded). Their most significant predator is the Bat Hawk (*Machaerhamphus*), some eagle-owls and snakes are also predators of bats. Hornbills, birds of prey and primates are all known to catch roosting bats.

The precise structure of wings, teeth, nose, ears, eyes and echo-location all have a direct bearing on the detection and capture of prey. Thus beetle-eaters have massive teeth and jaws while mosquito- and moth-eaters have smaller ones. Crepuscular hunters tend to have large eyes whereas miniature gnat-eaters have the smallest, fur-blinkered eyes. Slow flyers, restricted to dense forests or swamps, have short, broad wings, while fast, open-air hunters have long, narrow, 'high-ratio' wings that rely on fast air speeds and a low weight-loading. At least one family (the mouse-tailed bats) combines a long, broad membrane between body and wrist, and a very long forearm with short fingers and outer membrane (a supposedly 'primitive' arrangement).

A significant bat division is between 'shouters' and 'hummers'. The former call through the mouth and have unadorned, typically mammalian faces. The latter, in contrast, possess nose-leaves of various shapes and emit 'beams' of sound through the nostrils. Among several major advantages, nasal signals do not interfere with feeding and drinking. The various elaborate nose and ear structures displayed by nasal signallers serve to create harmonics and help control and shape both emission and reception of sound.

Two major types of sonar signals can be identified. In the first instance the major component of the signal has a constant frequency so that these are termed CF signals. In the second instance the frequency is modulated and these are called FM signals. Low frequencies and longer pulses below about 50kHz are mostly emitted by fast fliers in the open air. Low-intensity FM signals at about 100kHz allow slow-flying bats to detect slow-moving prey in an environment full of obstacles. No device yet invented by humans has achieved a fraction of this spatial charting nor approached its sensory sophistication.

Bats display a variety of anatomical, physiological and behavioural adaptations that are independent of those required for nocturnal flying and hunting. For example, flattened skulls, folding ears and peculiar sensory hairs are typical of crevice-dwellers. In general, nasal signalers roost hanging passively from hooked toes on long, tendinous legs with vestigial muscles whereas many simple-nosed insect bats have retained more versatile legs.

Bats often roost in houses or caves where they may come into close contact with people. Bed-bugs (*Cimex*) are bat parasites that have taken to humans as a secondary host. Many species of mites, ticks, flies and fleas are unique to particular bat hosts, as are many very localised viruses. Spores of fungi, such as *Histoplasma*, can proliferate in bat guano and can cause illness in humans when inhaled. Bats play an enormously important role in controlling insects. There are caves in Africa that shelter millions of bats and their denizens capture many tonnes of insects nightly. A single such cave can yield thousands of tonnes of phosphate-rich guano.

The biological status of bats is virtually unknown for most species, although several species are very localised and undoubtedly rare. In regions where other wild foods have been exterminated, people are increasingly turning to bats as food, a special hazard for the rarer bats.

FRUIT BATS PTEROPODIDAE

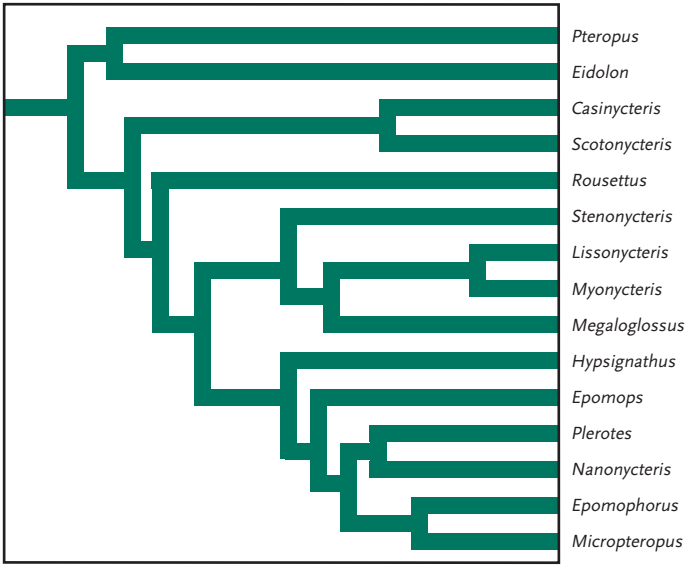
Flying-foxes	*Pteropus* (2 species)
Straw-coloured Fruit Bat	*Eidolon helvum*
Tear-drop Fruit Bat	*Scotonycteris zenkeri*
Golden Fruit Bat	*Casinycteris* (3 species)
Egyptian Rousette	*Rousettus aegyptiacus*
Mountain Fruit Bat	*Stenonycteris lanosus*
Angolan Soft-furred Fruit Bat	*Lissonycteris angolensis*
Collared fruit bats	*Myonycteris* (3 species)
Nectar Bat	*Megaloglossus woermanni*
Hammer-headed Fruit Bat	*Hypsignathus monstrosus*
Singing fruit bats	*Epomops* (3 species)
Benguela Fruit Bat	*Plerotes anchieta*
Flying Calf	*Nanonycteris veldkampi*
Dwarf epauletted fruit bats	*Micropteropus* (2 species)
Epauletted fruit bats	*Epomophorus* (6 species)

RECOGNITION Large brown eyes in a long, lemur-like head and broad, crepe-textured wings (with claws on the first and second digits) are the most notable peculiarities of fruit bats. Other features include powerful, hook-like claws on the toes, blunt, simple teeth and muscular tongues.

The repetitive chinking advertisement calls of males are highly characteristic (but often mistaken for those of frogs). Their chattering while feeding on fruits or flowers is somewhat like that of quarrelsome monkeys. Their eye-shine will reflect in torchlight but less reliably than that of carnivores or bushbabies.

GENEALOGY Fossil fragments of skulls and teeth bear such a resemblance to those of lemurs that even experts have confused them. Currently the earliest fossil dates from about 30 mya, by which time fruit bats had achieved an essentially modern form.

Among living species, rousette bats (*Rousettus*) and flying-foxes (*Pteropus*) are the most conservative, with a complement of 34 teeth and exceptional abilities in clambering through



Tentative phylogenetic tree for fruit bats (partly after Giannini & Simmonds 2003, and Almieda *et al.* 2011).

tangles of vegetation. Among the most derived is the Nectar Bat, *Megaloglossus woermanni*, which is adapted to hover and extract nectar from flowers.

GEOGRAPHY Fruit bats probably evolved in South-East Asia, where the greatest variety and range of forms still exist. In Africa there is a clear division between equatorial rainforest species (the centre–west realm) and south–east realm species. Rousette bats, a mainly Asiatic group, span both regions, and the flying-foxes, another Asiatic group, occur only on Indian Ocean islands off Africa.

ECOLOGY Fruit bats are entirely dependent on a year-long supply of fruits and flowers. They have large tongues, blunt, short teeth and a deeply ridged palate which, working together, crush, squeeze and rasp fruits so that only juice and pulp are swallowed. Fibres, seeds and rind are usually spat out.

Fruit bats that visit arboreal flowers for nectar sometimes act as important pollinators. Where they destroy the flowers these are usually super-abundant and adapted to such attrition. Almost all fruit bats disperse seeds by picking fruit in one tree and 'processing' or excreting its seeds in another. In cleared or open habitats fruit bats are important agents in reafforestation. Isolated trees or thickets, such as those on termitaries, provide both perches for the bats and a bed protected from fire, sun and floods for the seeds which they drop.

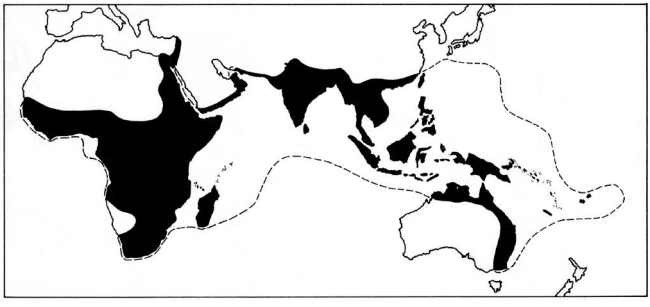
There are several species of very common fruit bats that only live in savanna regions. This indicates how rich these habitats are in fruits but the bats are obliged to migrate or 'camp' in order to maintain a continuous fruit supply. People living in south-eastern Africa are as familiar with the comings and goings of fruit bats as Europeans and Americans are with migrant birds but, sadly, have made scant effort at documentation.

NATURAL HISTORY The need to maintain or regain contact despite seasonal shifts and nightly dispersal over wide ranges has led to the evolution of species-specific calls that carry well, even in heavily wooded country. The most audible, frequent and persistent callers are epomophorine bats (the main exclusively African radiation). In several species belonging to this group male calls are synchronised with emissions of scent from the glandular pockets that contain their epaulettes. The name *Epomophorus* refers to a tuft of brilliant white fur, growing on the point of the shoulder, which opens out and dispenses scent each time the diaphragm contracts. The muscular spasms that accompany the male's loud call evert the shoulder pouch and so allow the bat to emit simultaneous signals in each of three separate channels: sound, scent and vision (see figures on p.336).

Many African fruit bat species form small social groups that find fruits independently; others form gigantic noisy roosts in trees or caves. Some species have developed very precise control (through prostaglandins) over the timing of their reproduction by delaying implantation of the future foetus. One species, the Straw-coloured Fruit Bat (*Eidolon helvum*), has now become an important research animal in the human quest for natural processes of birth control.

Sexual behaviour is initiated by females advertising their presence and condition. The young are born blind but otherwise well developed and with disproportionately large feet. Adult females have 'false-nipples' as well as milk-bearing teats, firm points of attachment for the infant.

ADAPTATIONS Fruit bats have large heads that accommodate their specialised sensory organs. Because fruits are found mainly by scent and also by sight, the nasal barrel is large, as are the eyes. The bats have large brains, large tongues, extrusive lips, a wide maw and flexible cheek pouches. The males of at least two species of singing fruit bats (*Epomops*) have even larger heads

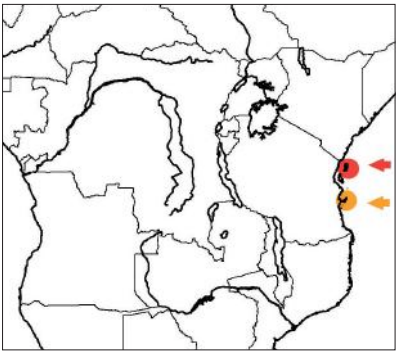


Global distribution of fruit bats.

because the apparatus for amplifying sound has enlarged the nasal area and demanded resonating sacs which inflate during calling.

Cave-dwelling Egyptian Rousette and Mountain Fruit Bats have developed an ability to fly in total darkness by clicking the tongue. Released in a blacked-out room these bats stop clicking the instant a light is turned on, and start again the moment it is extinguished. This crude form of echo-location seems to be the 'improvisation' of cave-dwellers and suggests that the fruit bat lineage diverged before techniques of echo-location had proceeded very far. The faces/skulls of dogs bred by artificial selection semi-mimic Natural Selection in fruit bats: Basenji (*Lissonycteris*), Boxer (*Casinycteris*) and Borzoi (*Megaloglossus*)!

P. comorensis



Flying-foxes

FLYING-FOXES *Pteropus*

MEASUREMENTS HB 220–265mm. FA 150–161mm. W 400–650g.

RECOGNITION Large, dark-winged fruit bats with yellowish or reddish heads and 'fox-like' or 'dog-like' faces. They roost exposed in large trees, usually in large colonies, and are restricted to oceanic islands. One aspect of this restriction is their habit of frequent 'skinny-dipping' in sea water, splashing their undersides during evening flights away from their day roosts.

SPECIES *P. voeltzkowi* (Pemba I.), *P. comorensis* (Mafia I.).

HABITAT Moist tropical islands in the Indian and Pacific Oceans.

FOOD Fruits and flowers.

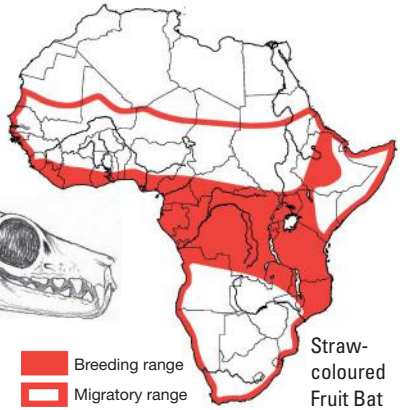
STATUS Endangered through human persecution and habitat loss.

P. comorensis

P. voeltzkowi

P. voeltzkowi

P. voeltzkowi



Straw-coloured Fruit Bat

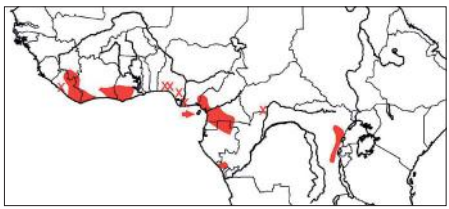
STRAW-COLOURED FRUIT BAT *Eidolon helvum*

MEASUREMENTS HB 150–195mm. FA 110–135mm. W 250–311g.
RECOGNITION A large, black-winged fruit bat with pale tawny fur on the back, shoulders and underside. Roosts mainly in large groups (sometimes in tens, even hundreds, of thousands) in open trees, often in towns or close to waterfalls or the sea. Conspicuous and high-flying, with long, tapered, but broad-based wings that carry it in strong, direct flight.
HABITAT Breeds in equatorial Africa but ranges all over sub-Saharan Africa outside the breeding season (including very dry and high montane areas). Breeding roosts are vacated 2 or 3 months after the birth season for about 3 months. Roosts are typically sited near noise (waterfalls and city streets are common choices). Noise may facilitate breeding.
FOOD Fruits, flowers, nectar, pollen, buds and occasionally young leaves.
STATUS Abundant and widespread.

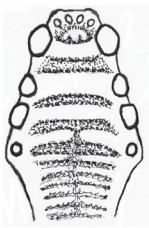
TEAR-DROP FRUIT BAT

Scotonycteris zenkeri

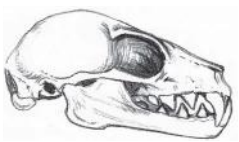
MEASUREMENTS HB 65–85mm. FA 47–55mm. W 16–24g.
RECOGNITION Prominent, tear-like white spots occur on either side of the eyes and others over the upper lip. Fur is variably tinted and wings are dark brown. Roost singly in vegetation.
HABITAT Lowland rainforests of West and central Africa; mostly found at lowest levels in undergrowth.
FOOD Fruits and flowers. Fruits are possibly gathered from the forest floor.
STATUS Rare and little known.

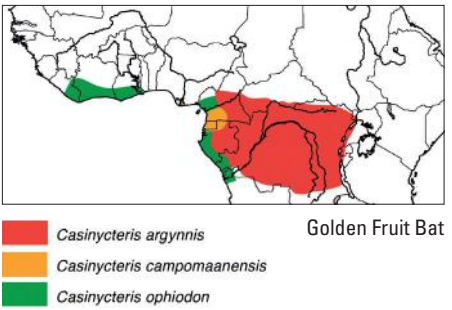


Tear-drop Fruit Bat



palatal ridges





Golden Fruit Bat

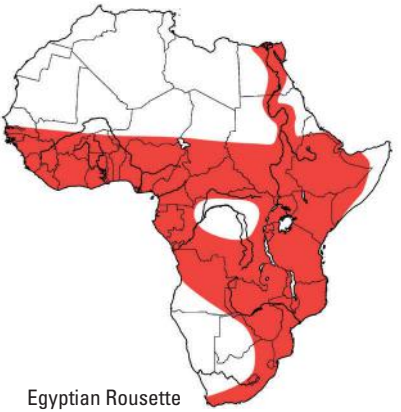
GOLDEN FRUIT BATS *Casinycteris*

OTHER NAMES Short-palated Fruit Bat.
MEASUREMENTS HB 90–95mm. FA 50–63mm. W 26–33g.
RECOGNITION Fruit bats with bold white margins to the mouth, eye and ear base. The hard palate is unlike other fruit bats in not extending back behind the tooth-row, implying that the fruit-squeezing action of the tongue and palate is modified in this species. Roosts singly or in pairs.
SPECIES *C. argynnis*, *C. campomaanensis*, *C. ophiodon*.
HABITAT Known from upper Guinea and the main lowland forest block between Liberia and E DR Congo. Recorded from low dense undergrowth.
FOOD Specialised feeding habits, in which fruits are processed mainly at the front of the mouth, would seem likely.
STATUS Currently among the least known of African fruit bats.

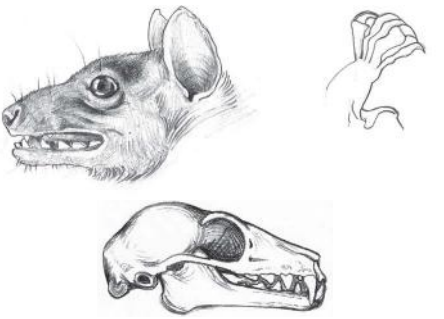
EGYPTIAN ROUSETTE

Rousettus aegyptiacus

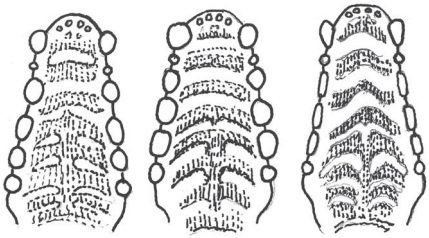
OTHER NAMES Egyptian Fruit Bat
MEASUREMENTS HB 109–192mm. FA 82–106mm. W 83–170g.
RECOGNITION A large, black-winged fruit bat with brownish-grey fur, dark crown, rounded ears and blunt muzzle. There is only a vestige of webbing between the fifth toe and the cartilaginous heel-spur. A cave-dweller, it is often very vocal.



Egyptian Rousette

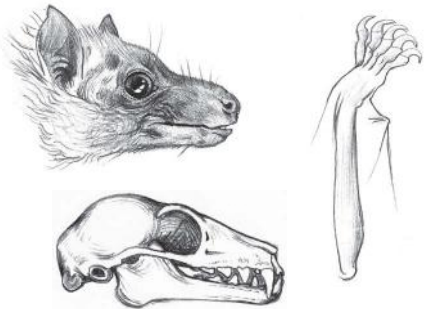


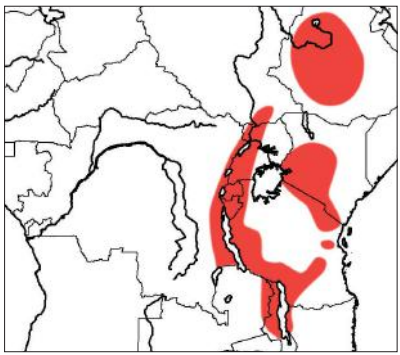
HABITAT Sub-Saharan Africa, E Mediterranean and S Arabia. From its cave roosts (where it often gathers in many thousands) it flies long distances to sources of fruits in a wide range of habitats.
FOOD Fruits, flowers, nectar and pollen; occasionally leaves and buds.
STATUS Widespread and common.



Lissonycteris angolensis *Rousettus aegyptiacus* *Stenonycteris lanosus*

palatal ridges





Mountain Fruit Bat

MOUNTAIN FRUIT BAT

Stenonycteris lanosus

MEASUREMENTS HB 114–173mm. FA 85–95mm. W 94–162g.
RECOGNITION A large fruit bat with black wings, shaggy, dark grey fur, pointed ears and a long but blunt-ended muzzle. A cave-dweller in montane areas.
HABITAT Montane forest areas in E Africa, Ethiopia and Madagascar.
FOOD Fruits, nectar and pollen.
STATUS Locally abundant but very sparsely distributed. Dependence on caves may require special protection for roosting sites. Echo-locates by means of tongue clicks.

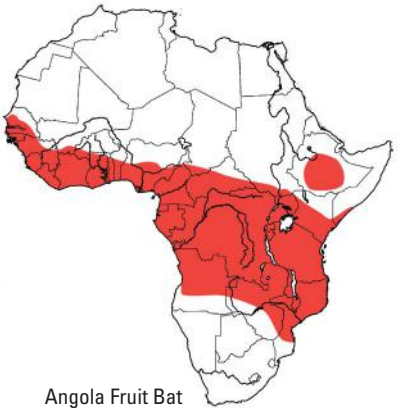
Mountain Fruit Bat Angola Fruit Bat

ANGOLA FRUIT BAT

Lissonycteris angolensis

MEASUREMENTS HB 105–135mm. FA 65–91mm. W 65–91g.
RECOGNITION A plain brown fruit bat with oval ears and a pointed nose at the end of a tapered muzzle. The patagium is attached to the second toe. Adult males have a 'collar' of sticky hair. Roosts singly or in small groups in low, thick vegetation, in hollow trees or near the mouths of caves, and is quiet and cryptic.
HABITAT Tropical Africa, mainly in forests at low and higher altitudes.
FOOD Fruits and flowers.
STATUS Common and widespread.

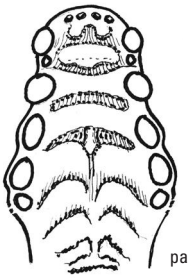
Angola Fruit Bat



Angola Fruit Bat

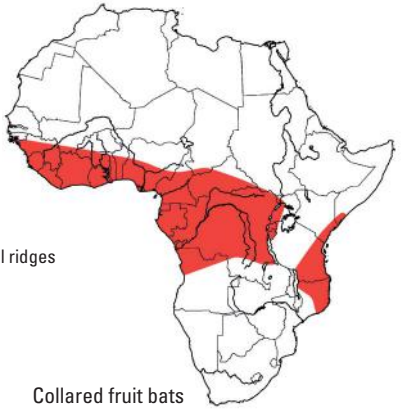
COLLARED FRUIT BATS *Myonycteris*

MEASUREMENTS HB 88–120mm. FA 55–70mm. W 35–80g.
RECOGNITION Brown or buff fruit bats with broad shoulder ruffs, or 'collars', in males. Pointed ears resemble those of the Angolan Fruit Bat but are smaller. Roost singly or in small groups in dense, low vegetation. Netted individuals resist capture, lunge , bite and chatter.
SPECIES *M. torquata* (Upper Guinea to Uganda), *M. relicta* (Indian Ocean, coastal forests, Kenya, Tanzania), *M. brachycephala* (São Tomé and Principe Is.).
HABITAT In or close to rainforest, including savanna–forest mosaics where the forest has become vestigial.
FOOD Fruits and nectar.
STATUS Tend to be rare and localised.



palatal ridges

M. torquata

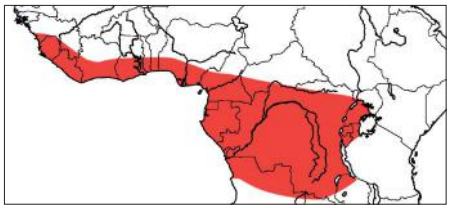


Collared fruit bats

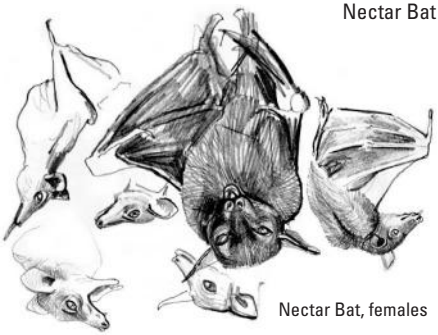
NECTAR BAT *Megaloglossus woermanni*

OTHER NAMES Woermann's Long-tongued Fruit Bat.
MEASUREMENTS HB 64–82mm. FA 40–46.5mm. W 12–20g.
RECOGNITION A very small fruit bat with an extremely fine-pointed muzzle and a very long, thin, brush-textured tongue. The soft pale fur appears to be 'smoked' with brown or sepia. Males have a ruff of stiff, pure white hair, apparently growing from a glandular patch. It

Nectar Bat, male



Nectar Bat



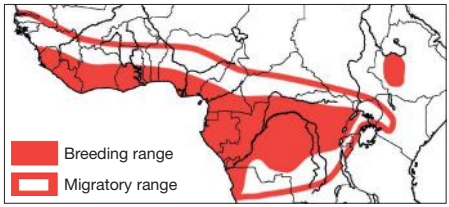
Nectar Bat, females

is apparently not very vocal. Two races have been described.

HABITAT Main forest blocks from Guinea to Uganda. Roosts in dense forest foliage and has been caught under banana fronds and in huts or houses within the forest. Has been netted flying along forest tracks bordered by flowering trees (*Spathodea*).

FOOD Nectar.

STATUS Very widely distributed.



Hammer-headed Fruit Bat

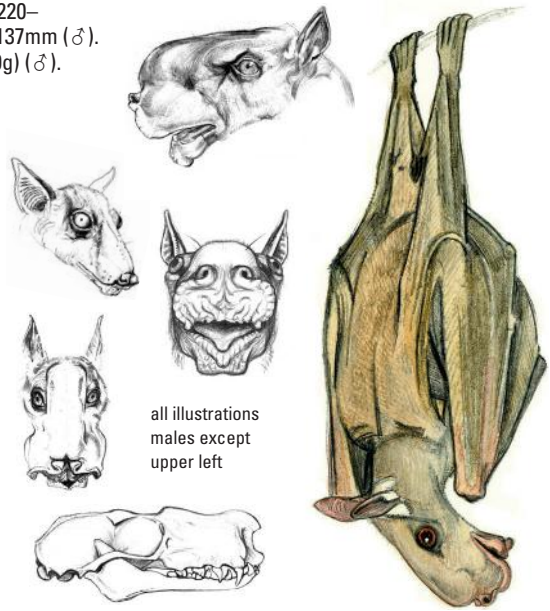
HAMMER-HEADED FRUIT BAT

Hypsignathus monstrosus

MEASUREMENTS HB 195–200mm (♀), 220–275mm (♂). FA 118–128mm (♀), 125–137mm (♂). W 250g (218–377g) (♀), 425g (228–450g) (♂).

RECOGNITION The largest continental African fruit bat, with brown fur and membranes and a yellowish-brown skin colour on the muzzle, ears and digits. Males are almost twice the weight of females and have inflatable sacs over the raised ridge of the nose and on each side of the neck. The male's lips are also modified to control sound and form a sort of crenellated rhinarium, or 'lip-disc'. Both sexes have tubular nostrils and white tufts at the base of the ears. Males make a very loud, explosive, blaring honk that only resembles other epomophorine loud calls from a distance. The call carries several kilometres on a still night.

DISTRIBUTION Throughout the lowland forest zone from Senegal to W



all illustrations males except upper left

Uganda. Seasonal excursions take individuals or small groups far beyond these limits (both north and south) and as far afield as W Kenya.

HABITAT Roosts at low levels in heavily shaded forests of almost all types, including mangroves and swamp forest but not montane areas. Some of its preferred foods are typical of secondary growth. Seasonal movements are poorly known and are probably influenced by fruiting patterns (and perhaps also by climate as it is sensitive to drops in temperature and stops calling in cool weather).

FOOD Soft fruits, especially wild figs and the fruit of Cabbage Trees or Forest Fever Trees (*Anthocleista*). Males have been known to fly up to 10km in search of concentrations of ripe fruits while females forage within a much more localised area (often on fruits of poorer quality).

BEHAVIOUR Females and their young form temporary associations of up to 20 animals but individuals move frequently and do not appear to form lasting attachments. The loud calls of adult males serve as acoustic beacons. Competitive assemblies of calling males, or 'leks', provide a point of reference for all Hammer-head Bats within an 8–10km radius and attract females, who make frequent visits before closing in on a particular female. Presumably the cumulative noise at the centre of the 'choir', as well as the volume and timbre of individual singers, influences the female's choice. In the equatorial bimodal climate there are two mating peaks that coincide with warm dry weather, at which time both sexes converge on the 'leks'. Gestation lasts 4 months and females often mate with an infant attached to them.

ADAPTATIONS Male hammer bats might almost be described as flying loudspeakers, so extensive is the structural modification of their organs towards production and resonance of noise. The larynx has displaced heart, lungs and diaphragm to fill the entire chest with an enormous curved structure like a tuba (see p.336). With the greatest mating success going to powerful singers near the centre of a 'choir', there has been strong sexual selection for large competitive singers.

STATUS Locally common.

SINGING FRUIT BATS *Epomops*

MEASUREMENTS HB 103–195mm. FA 77–102mm. W 65–158g.

RECOGNITION Medium-sized brown fruit bats with white tufts at the base of the ears and broad, blunt muzzles. Vocalisations very loud and 'musical'.

SPECIES *E. franqueti* (Liberia to Uganda and Angola), *E. buettikoferi* (Guinea to Nigeria), *E. dobsoni* (Angola to Tanzania and Malawi).

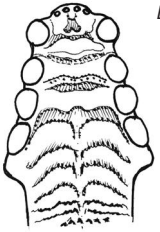
HABITAT Forests and forest–woodland mosaics.

FOOD Fruits and nectar.

STATUS *E. franqueti* is common and widespread. Other species are insufficiently known.

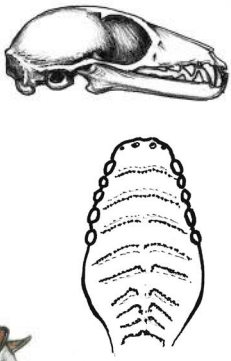
Singing fruit bats

E. franqueti

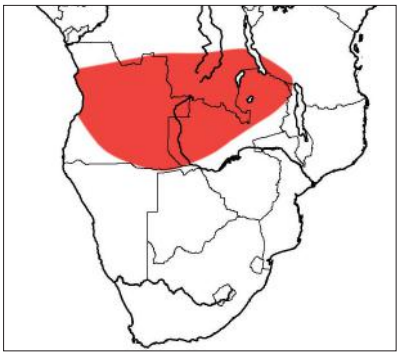


palatal ridges

E. franqueti, male (*left*) and female (*above*)



palatal ridges



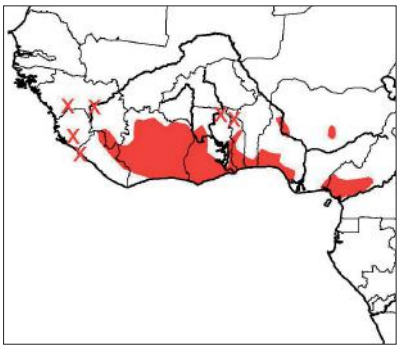
Benguela Fruit Bat

BENGUELA FRUIT BAT *Plerotes anchietae*

OTHER NAMES Anchieta's Broad-faced Fruit Bat.
MEASUREMENTS HB 70–96mm. FA 47–53mm. W 20g.
RECOGNITION A beautiful, pale fawn-grey, tailless fruit bat with a peculiar 'moustache' and 'beard' of stiffened hairs around the mouth and rather long, crinkled fur on the lower back and legs. When wrapped around the body, the elegantly patterned wings present perfect mimicry of a scorched or smutty dead leaf. There are areas of white fur around the base of the ears. Lacks a cartilaginous spur on the heel and the caudal margin of the legs carry a mere vestige of web. The muzzle is unusually broad, flat and shallow with very rudimentary teeth – perhaps a structure well suited to generating a strong sucking action. Pouches around the eyes of males have been reported and suggest an unusual loud call but other investigators have been unable to find or confirm such pouches. Naturalists encountering this species should closely observe the bats' behaviour and morphology to help resolve this question.
HABITAT Southern margins of the Congo basin between the Atlantic and Lakes Tanganyika and Malawi (Nyasa). Probably forest mosaics and riverine strips.
FOOD Extrapolating from palate and tongue, very soft fruit, nectar, pollen and, perhaps, insect honeydew and associated sugars and proteins.
STATUS One of the more interesting yet least known of African fruit bats.

FLYING CALF *Nanonycteris veldkampi*

OTHER NAMES Veldkamp's Epauletted Fruit Bat.
MEASUREMENTS HB 69–87mm. FA 46–54mm. W 16–36g.
RECOGNITION Very small, fawn-brown fruit bat with a slender muzzle and large eyes. Thick, soft fur covers the back and legs and extends onto the membranes. There is a short white 'moustache' and white tufts of fur at the base of the ears. Males have white 'epaulettes'. May congregate at feeding sites.
HABITAT Senegal to E DR Congo in lowland rainforest and forest mosaics.
FOOD Nectar and pollen.
STATUS Rarely seen and little known.



Flying Calf

palatal ridges

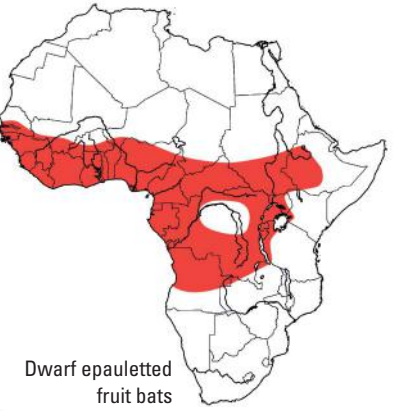
Flying Calf

M. pusillus

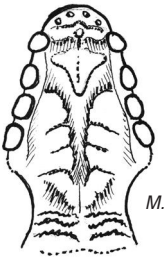
DWARF EPAULETTED FRUIT BATS

Micropteropus

OTHER NAMES Lesser epaulette fruit bats.
MEASUREMENTS HB 67–103mm. FA 46–67mm. W 25–40g.
RECOGNITION Small, tawny fruit bats with white tufts at the base of the ears and white 'epaulettes' on adult males. The short muzzle has prominent nostrils. Males make a shrill, chinking call which they repeat monotonously. Roost singly or in small groups in shady vegetation.
SPECIES *M. pusillus* (encircles forest blocks), *M. intermedius* (Angola and DR Congo).
HABITAT Woodlands, savannas and forest mosaics outside the main lowland forest blocks.
FOOD Fruits, nectar and pollen.
STATUS *M. pusillus* is common and widespread. The status of *M. intermedius* is not known.



Dwarf epaulette fruit bats



palatal ridges

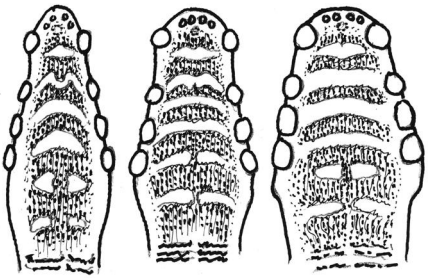
M. pusillus

palatal ridges

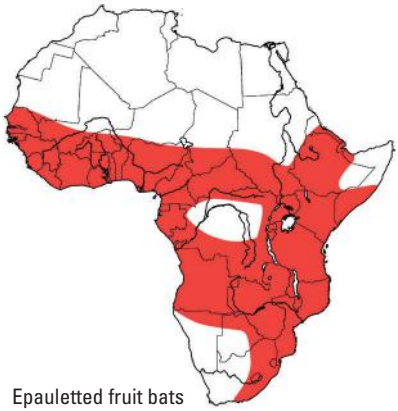
EPAULETTED FRUIT BATS

Epomophorus

MEASUREMENTS HB 96–170mm. FA 54–100mm. W 40–120g.
RECOGNITION Variably tinted, brown fruit bats of differing sizes. All have tufts of white fur at the base of the ears. Males have white 'epaulettes' on their shoulders. Utter chinking, frog-like calls.
SPECIES *E. gambianus* (Senegal to Ethiopia and South Africa), *E. labiatus* (Nigeria to Ethiopia to



E. gambianus (narrow) *E. wahlbergi* (medium) *E. labiatus* (broad)

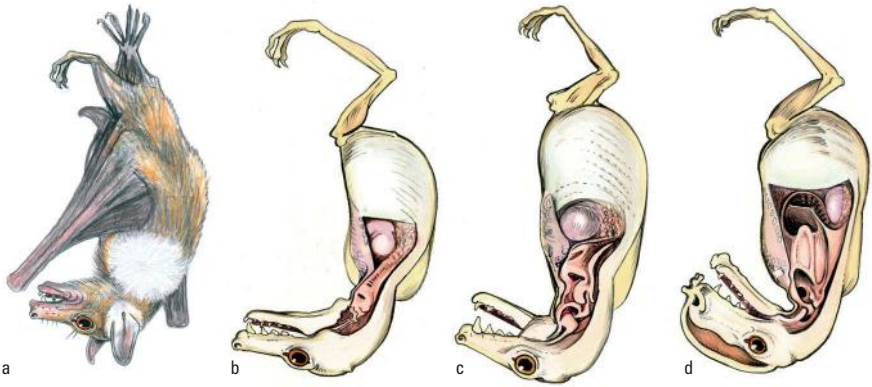

Epauletted fruit bats

Malawi), *E. minimus* (Ethiopia to Tanzania), *E. angolensis* (Namibia and Angola), *E. grandis* (Congo R. mouth region), *E. wahlbergi* (East and central Africa to Cameroon).

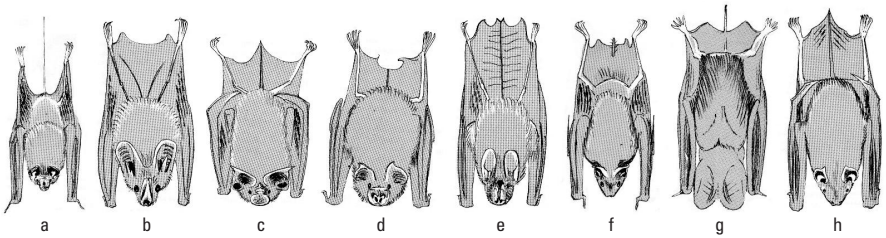
HABITAT Mainly savannas, woodlands and forest mosaics. Some species occur in main forest zones.

FOOD Fruits, flowers, nectar, pollen.

STATUS Most species are common and widespread, but status is generally unknown.



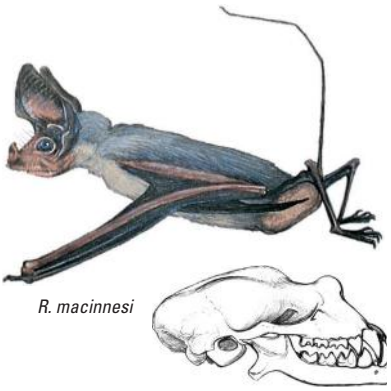
The evolution of a flying loud-speaker. Shape determined by signal-generating apparatus. Bisections of heads and thoraxes of: (a) & (b) *Epomophorus*, showing some elaboration of the vocal tract and eversion of the white 'epaulette' signal. (c) *Epomops*, showing significant enlargement of larynx. (d) *Hypsignathus*, showing larynx enlargement has displaced the entire chest cavity.



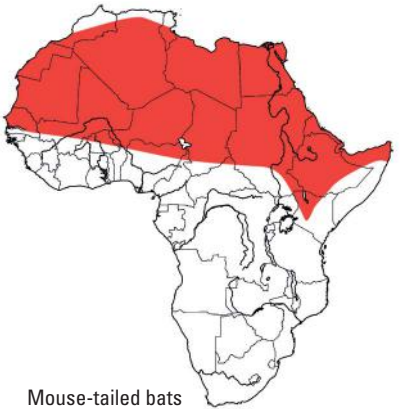
Insect-bat families: (a) mouse-tailed, (b) large-winged, (c) horseshoe, (d) leaf-nosed, (e) slit-faced, (f) sheath-tailed, (g) free-tailed, (h) long-fingered, vesper and pimple-winged.

MOUSE-TAILED BATS RHINOPOMATIDAE

The family consists of the single genus *Rhinopoma* with three species. Mouse-tailed bats have extremely slender limbs, a whip-like tail, and fat deposits at the root of the tail that wax and wane. When the bats are excited, the facial glands ooze secretions: roosts are strongly smelly. In several respects mouse-tails are one of the most primitive of bats. They have the shortest fingers, relative to the forearm, of any bats and they are poor fliers and tire quickly. Their echo-locating skills also seem less developed. However, modest flying abilities come with a set of physiological adaptations that allow them to live in very hot, arid, desert regions.



R. macinnesi



Mouse-tailed bats

MOUSE-TAILED BATS *Rhinopoma*

MEASUREMENTS HB 53–81mm. T 52–85mm. FA 45–74mm. W 5–37g.

RECOGNITION Sandy-coloured bats with long, wispy tails and valvular nostrils set in a small, pad-like nose-leaf. A membrane joins the large, rhomboid ears above the large, prominent black eyes. There are fat deposits around the base of the tail and hindlimbs. At rest the forearm is strikingly long and thin.

SPECIES *R. hardwickii* (mainly true deserts from Morocco to Arabia), *R. microphyllum* (mainly subdeserts and Sahel from Senegal to Nile valley and South-East Asia). A third species, R. *macinnesi* (formerly regarded as a subspecies of *R. hardwickii* and represented here) seems to be a little-known relict population from around the margins of the Ethiopian Dome.

HABITAT Desert and subdesert. Has an unusual tolerance for low humidity, high temperatures and relatively unprotected shelters, such as rock walls, houses, wells, tombs and caves. Generally lives in small, scattered groups of mixed sexes (10–100) but all-male and all-female groups are also known and may aggregate into flocks of thousands.

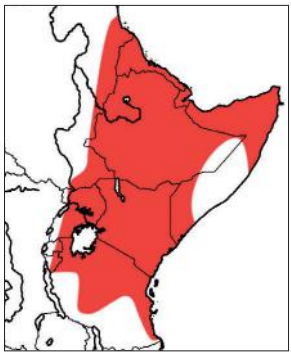
FOOD Mouse-tails hunt small desert insects and beetles with undulations of fast flapping interspersed with swoops and glides at 5–10m. Fat deposits fluctuate, implying seasonal shortages of food.

STATUS Widespread desert group.

LARGE-WINGED BATS MEGADERMATIDAE

Heart-nosed Bat	*Cardioderma cor*
Yellow-winged Bat	*Lavia frons*

RECOGNITION Broad-winged, large-eared, large-headed bats with ornate nose-leaves, thin, strut-like legs and long, silky fur. Restricted to Old World tropics and Australasia, these are large-eyed bats that often emerge before dark to hunt invertebrates from habitually used perches where they may be relatively conspicuous, a conspicuousness also advertised by territorial vocalisations equivalent to bird song. Also sometimes known as false vampire bats.



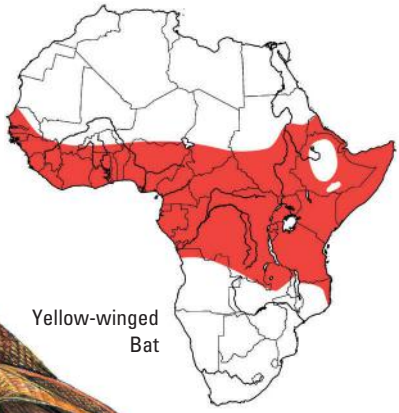
Heart-nosed Bat

HEART-NOSED BAT *Cardioderma cor*

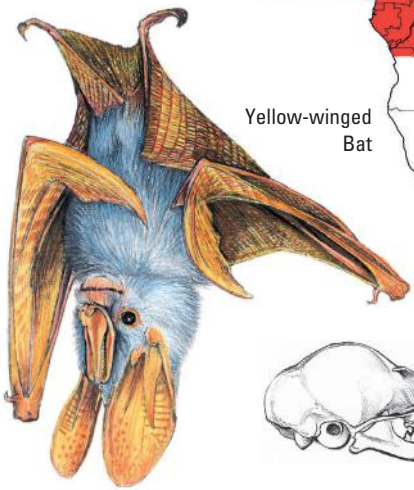
MEASUREMENTS HB 70–77mm. FA 54–59mm. W 21–35g.
RECOGNITION Relatively large bat with long, pale fur and joined ears bearing sharp, two-pointed ear tragi. The prominent muzzle is surrounded by a heart-shaped nose-leaf.
HABITAT Restricted to NE Africa and its coasts from Eritrea to central Tanzania. The Rift Valley, dry *Acacia* bush and the coastal littoral are preferred habitats. Uses houses for shelter but is shy and prefers dry caves. Roosts in groups of 3–100 or more.
FOOD Invertebrates and, more occasionally, vertebrates (including other bat species), hunted from a limited number of lookout posts on the lower, outer margins of trees or bushes. After forays, prey is brought back to be eaten at the perch or even to the day-time shelter, where debris collects below the roost. Habitually used perches serve not only as hunting perches but advertise territories uttering pulses and twitters with complex harmonics.
STATUS Although locally common this is a sparsely and irregularly distributed species that might be vulnerable to habitat change.

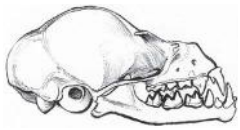
YELLOW-WINGED BAT *Lavia frons*

MEASUREMENTS HB 63–83mm. FA 49–65mm. W 16–36g.
RECOGNITION Very colourful bat with large black eyes, pale blue-grey fur and bright yellow-orange membranes and ears; tailless. Wings exceptionally broad and ears long, with a spiky tragus. Elongated nose-leaf also encloses a pointed sella, or spike, that runs down its centre. Often roosts in light shade in large savanna trees (especially *Euphorbia* in the dry season). Changes roosting site easily and frequently; may hunt insects in evening or after dawn. A bird-like contact call.
HABITAT Low-lying savannas, open woodlands, especially *Acacia*, and narrow forest galleries in tropical Africa, especially along rivers and lakeshores. Perching and roosting sites, often spaced out in pairs, and typically close to insect concentrations. When hanging quite still it resembles a dead leaf but is usually alert and active most of the day.



Yellow-winged Bat

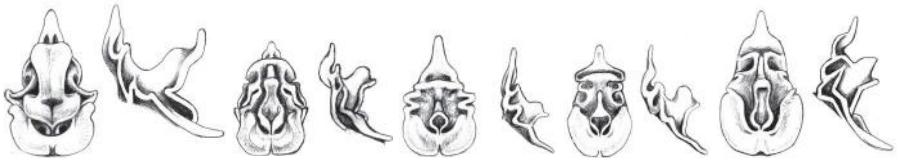




FOOD Invertebrates, notably swarming species such as termites, locusts, lake flies and mosquitoes. Occasional vertebrate prey suggested; known to chase other bat species.
STATUS A widespread and common species, taken by raptors, hornbills and snakes. Apparently able to startle potential predators with its brilliant colouring.

HORSESHOE BATS RHINOLOPHIDAE

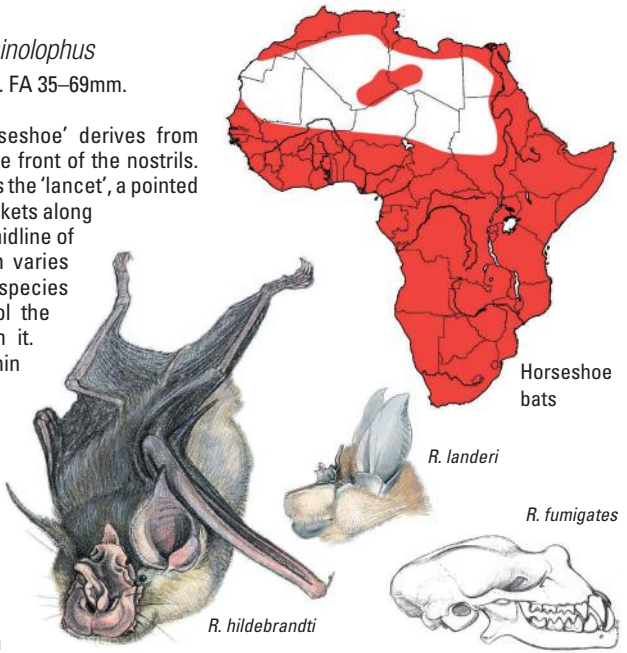
Widely distributed in tropical and temperate regions, 27 of some 77 species occur in Africa where several distinctive species-groupings have been identified. Elaborate nose-leaves and broad, leaf-shaped ears are directed towards a very effective type of CF sonar. Some phalanges of the fingers are reduced and rhinolophids are unique in having a rigid ring at the top of the chest formed by the fusion of the first ribs and first dorsal vertebra. Highly evolved and specialised bats, known from fossils to be very ancient. One scatter of apparently relict species, the *maclaudi* group, occurs across the Old World, mostly as rare, localised species in highland refugia. Species belonging to the *ferrumequinum* and *euryale* groups are mostly restricted to north of the Sahara but some species have colonised temperate South Africa. The *capensis* group also range mainly across southern temperate Africa. The *fumigates* group also has a southern and eastern bias. Only the *landeri* group has a strong centre–west equatorial forest focus. Relict and North African groups apart, each of these groups has one species that is exceptionally widespread, implying that each grouping possesses its own form of specialisation. These bats provide rich topics for future research.



Highly diagnostic nose leaves of various *Rhinolophus* species and species groups.

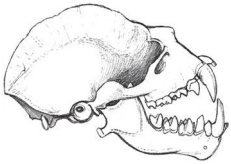
HORSESHOE BATS *Rhinolophus*

MEASUREMENTS HB 39–94mm. FA 35–69mm. W 5–33g.
RECOGNITION The name 'horseshoe' derives from a flat leaf that loops round the front of the nostrils. Behind it and above the eyes is the 'lancet', a pointed leaf with complex folds or pockets along its sides. Emerging from the midline of the nostrils is a sella, which varies in shape from species to species and clearly serves to control the sound emitted from beneath it. The sella is supported by a thin wall in the midline plane, known as the 'connecting process'. All horseshoe bats have nose-leaves of a similar structure but the proportions and shapes of their component parts are distinctive in each species and provide a convenient aid to identification. All species hang by their hindlegs when



at rest. The wings are wrapped around the body while the tail is folded back over the rump.
SPECIES (*maclaudi* group) *R. maclaudi*, *R. hilli*, *R. ruwenzorii*, *R. ziama*; (*ferrumequinum* and *euryale* groups) *R. darling*, *R. clivosus*, *R. hillorum*, *R. deckenii*, *R. hipposideros*, *R. euryale*, *R. meheleyi*, *R. sakejiensis*; (*capensis* group) *R. capensis*, *R. swinnyi*, *R. simulator*, *R. maendeleo*, *R. adami*; (*fumigates* group) *R. fumigates*, *R. hildebrandti*, *R. eloquens*; (*landeri* group) *R. landeri*, *R. alcyone*, *R. blasii*, *R. denti*, *R. eloquens*, *R. guineensis*, *R. silvestris*.
HABITAT Species-groups and species show some geographical and ecological preferences, otherwise all vegetation types. Horseshoe bats generally prefer to hunt in sheltered areas and roost in caves, holes, buildings, hollow trees. Temperate species choose warm roosts when active but retreat to cool, damp sites when torpid.
FOOD Varies from species to species. Mosquitoes, moths, beetles, spiders and scorpions are caught in flight, by foraging at low levels or by ambush on the ground.
STATUS The life histories of most species are virtually unknown.

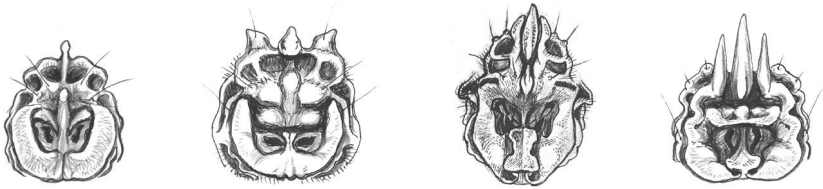
Hipposideros gigas



LEAF-NOSED BATS HIPPOSIDERIDAE

Leaf-nosed bats	*Hipposideros* (14 species)
Trident leaf-nosed bats	*Asellia* (2 species)
Percival's Trident Bat	*Cloeotis percivali*
African Leaf-nosed Bat	*Triaenops afer*

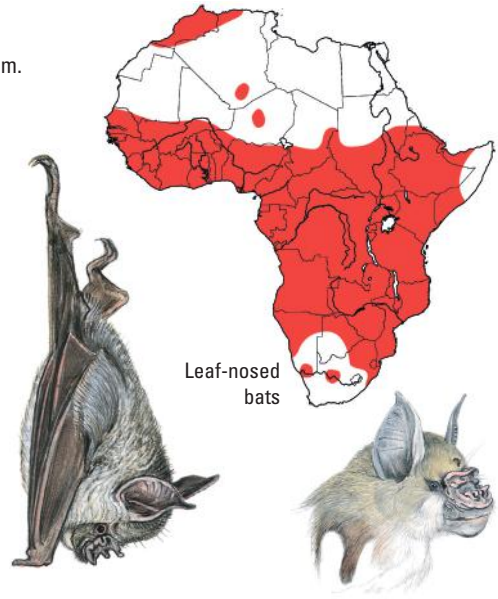
Bats of this family are related to horseshoe bats but leaf structures differ (see illustration).



Nose-leaf structures for leaf-nosed bats: (a) *Hipposideros cyclops*, (b) *Asellia*, (c) *Triaenops* and (d) *Cloeotis*.

LEAF-NOSED BATS *Hipposideros*

MEASUREMENTS HB 37–136mm. FA 34–124mm. W 6–138g.
RECOGNITION A very diverse group of bats with leaf-shaped ears and less elevated nose-leaves than horseshoe bats. Many have broad, scroll-like folds and flanges above the eyes and the sides of the muzzle often bear a series of very shallow lappets 'stacked' outside the rim of the main 'horseshoe' that surrounds the nostrils. The eyes are small but functional and leaf-nosed bats in a well-lit roost will watch an intruder attentively in addition to emitting bursts of ultrasound. They prefer to hang free from the ceilings of caves or house lofts, or in tree hollows. In some species males roost alone for much of the year; others form small



Right: H. cyclops; far right: H. commersoni

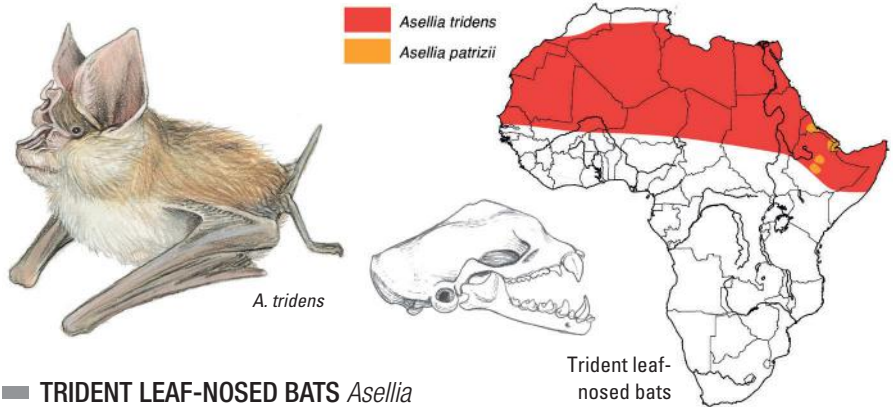
parties, yet others congregate in many thousands. Predominantly tropical Asian (with Africa a relatively marginal area: 53 species are non-African). However, widely separated representatives living in South-East Asia and Africa imply more than one past connection. The main African radiation concerns the 'bicolor sub-group' in which the *caffer*/*ruber* sibling species are of special interest for their evolution having taken place within Africa. Once lumped together because they are so similar, *H. caffer* and *H. ruber* overlap extensively, yet their differences must originate in past geographic separation. *H. ruber*'s origins are most likely in the centre–west tropical forests while *H. caffer* is more likely from the south–east realm.

SPECIES *H. megalotis*: probable relic of very early *Hipposideros* population. (*cyclops* group: *some conservative Asian species similar) H. cyclops, H. camerunensis*; (*speoris* group: later Asian immigrant) *H. abae*; (*commersoni* group: widespread giant forms, formerly treated as subspecies of *H. commersoni*) *H. vittatus, H. gigas*; (bicolor group: African radiation) *H. beatus, H. caffer, H. ruber, H. curtus, H. fuliginosus, H. jonesi, H. lamottei, H. marisae*.

HABITAT Forests, woodlands and savannas at low and medium altitudes. Some species (*H. cyclops, H. camerunensis, H. abae*) are strictly forest bats. *H. megalotis* is a dry upland species.

FOOD Diverse sizes and habitats are matched by diverse feeding habits. Beetles, cicadas, termites, moths, crickets, cockroaches, ants and woodlice have been recorded for this group. Prey is caught in flight or is snatched off leaves or litter by quartering in slow, wavering flight close to the ground.

STATUS The Large-eared Leaf-nosed Bat (*H. megalotis*) is known to be very rare and localised. Most other species have wide ranges. Intensive tree-felling may locally eradicate some forest species by eliminating the large hollow trees in which the bats roost.



TRIDENT LEAF-NOSED BATS *Asellia*

MEASUREMENTS HB 50–62mm. FA 38–55mm. W 3.4–13g.

RECOGNITION Small, pale bat with broad, pointed ears and a squat nose-leaf with three blunt protuberances on its posterior margin. These surmount six 'cells', or pockets, that form the crenellated upper margin of the nose-leaf. The skull and back bone are also unique.

SPECIES *A. tridens* (Sahara to Pakistan), *A. patrizii* (S Red Sea).

HABITAT Deserts and Sahelian subdeserts, roosting in dark ruins, wells and caves, often in many hundreds.

FOOD Desert insects and scorpions.

STATUS Poorly known.

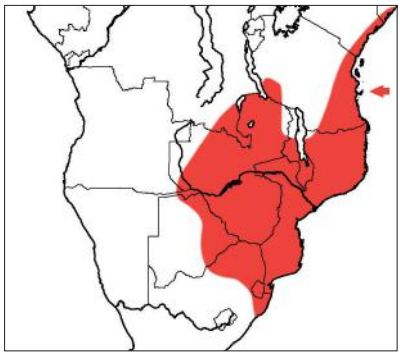
PERCIVAL'S TRIDENT BAT

Cloeotis percivali

MEASUREMENTS HB 36–40mm. FA 32–39mm. W 3–6g.

RECOGNITION A very small, pale bat with yellowish, orange and buff morphs. Underside is pale off-white. Ears are very small and rounded. Wings

are dark. The nose-leaf has three prominent points arising from the posterior margin of the nose-leaf.
HABITAT A species of the south–east realm, patchily distributed, mainly in low-lying woodlands and savannas, sometimes coastal. Roosts in the darkest recesses of caves and mines. Forms dense clusters, from small groups to several hundred individuals.
FOOD Small insects, especially moths.
STATUS Poorly known.

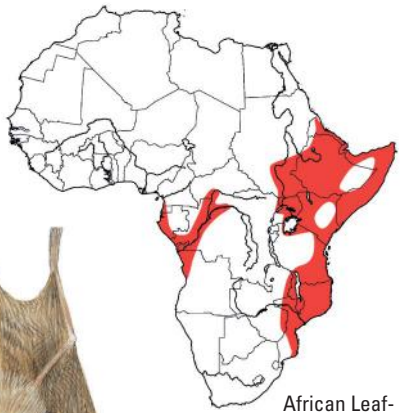


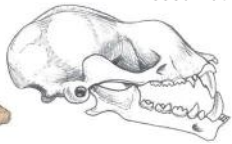
Percival's Trident Bat

AFRICAN LEAF-NOSED BAT

Triaenops afer

MEASUREMENTS HB 50–57mm. FA 50–55mm. W 8–15g.
RECOGNITION Compact leaf-nosed bat with rounded ears, half-buried in fur, with short projecting tips. Back of nose-leaf has three spear-shaped leaves: small fourth spear projects from centre of nose-leaf. Accessory leaflets, or 'scrolls,' surround the large, deep-set nostrils. Long, narrow head disguised by long, dense, grey, brown or rich russet red fur. Wings dark brown. Often found in large colonies where individuals hang close together but avoid actual contact.
HABITAT A mainly coastal species of NW Indian Ocean littoral but ranges up large river valleys inland to uplands, notably the Ethiopian Dome.
FOOD Small insects caught in slow, moth-like flight.
STATUS Widely distributed and locally abundant.





African Leaf-nosed Bat

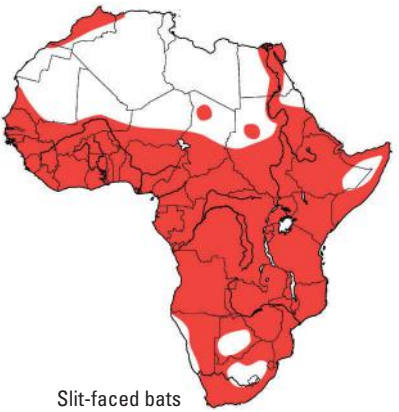
SLIT-FACED BATS NYCTERIDAE

The family comprises one genus, *Nycteris*, with 12 species. The name derives from a trench running back from the nostrils into a broad dish above very small, but still functional eyes and below the very long funnel-shaped ears (with small, club-shaped tragi). On either side of this trench there are sculpted leaves that control or channel sound back to the forehead dish and possibly into the ears. This foliated trench has a simpler structure in one species cluster (*arge* group) and progressively more complex folds and elaborations in other groups, suggesting that ever-greater sound control and spatial manoeuvrability has been evolving in nycterids. The tail terminates in a cartilaginous T- or Y-shape that is unique to this group. These bats are slow foragers, with a moth-like flight. The nycterid radiation seems to be mainly African.

All four of the species with least developed nose-leaves (*arge* group) are restricted to the centre–west equatorial forest zone, suggesting that this may be the region and habitat of origin for *Nycteris*. An expansion into less strictly forested habitats is implied by the three species of the *hispida* group. Of these, *N. aurita*, is restricted to eastern Africa and may represent a linking form. Another is a 'giant' species, *N. grandis*. The most widespread group and species, *N. thebaica*, seems to owe its

pan-African range to a tolerance of cooler, drier and more mountainous habitats and to versatility of diet and hunting techniques. These skills, together with exceptional manoeuvrability on rounded, sail-like wings, may help explain the broad range and ecological versatility of *N. macrotis*, the species with most elaborate nose-leaves and a pan-tropical distribution.

SLIT-FACED BATS *Nycteris*


Slit-faced bats

MEASUREMENTS HB 43–85mm. FA 32–65mm. W 5–43g.

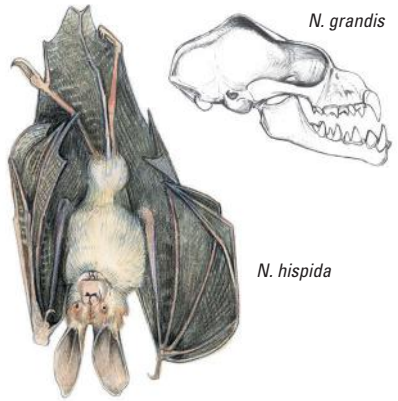
RECOGNITION Large-eared, broad-winged bats with silky fur and a long tail fully enclosed in membrane with a T- or Y-shaped tip. The nose trench, or slit, is surrounded by a series of beautifully sculpted lobes and flanges, which must modulate and control their high-frequency 'whispers'. Prefer to roost in cool, dark and, ideally, moist retreats within caves, holes, hollow trees, buildings or culverts but some species will tolerate dense, dark foliage or tangled, shady thickets (notably on termitaries). Roost individually or in groups of up to hundreds (*N. thebaica*). Flight is very acrobatic; if they meet an obstacle in dense vegetation they momentarily perch before taking off again.

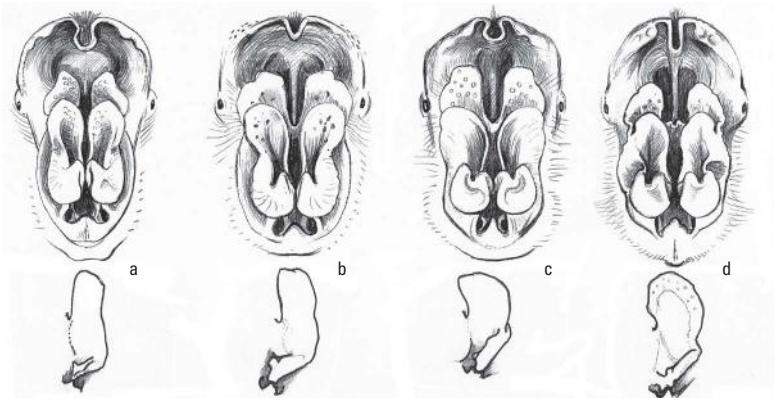
SPECIES (*arge* group) *N. arge*, *N. nana*, *N. intermedia*, *N. major*; (*hispida* group) *N. hispida*, *N. grandis*, *N. aurita*; (*thebaica* group) *N. thebaica*, *N. gambiensis*; (*macrotis* group) *N. macrotis*, *N. parisi*, *N. woodi*.

HABITAT Found in a wide range of vegetation types but forage at low levels in areas of dense undergrowth, reeds, thickets, mangroves, etc., all over Africa except open desert.

FOOD Crickets, grasshoppers, moths, flies, cicadas, flying termites. Various larger insects, spiders and scorpions are plucked off vegetation, the ground, or caught in flight. Slit-faced bats emerge late and retire early.

STATUS All species are widely distributed in both forest and other ecotypes.



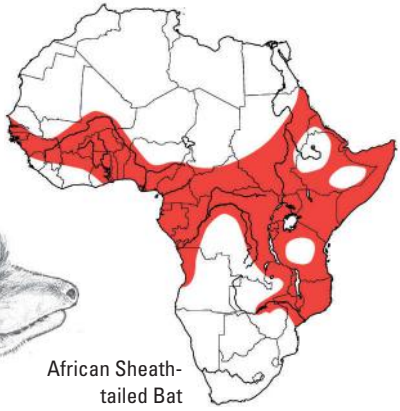


Nose-leaf structures (*above*) and shape of ear sella (*below*) of various *Nycteris*: (a) *N. nana*, (b) *N. hispida*, (c) *N. macrotis* and (d) *N. thebaica*.

SHEATH-TAILED BATS EMBALLONURIDAE

African Sheath-tailed Bat	*Coleura afra*
Tomb bats	*Taphozous* (5 species)
Black-hawk Bat	*Saccolaimus peli*

A family of simple-nosed bats most easily identified by the half-sheathing of their tail within the interfemoral membrane. All species have large eyes and an alert demeanour and possess strong-smelling glands, usually enclosed in a throat sac. Throat scents are wafted at conspecifics during courtship rituals that include static wing-fanning. They are considered to be among the more primitive of insect bats but are very successful, ranging right around the world in the tropics and subtropics.



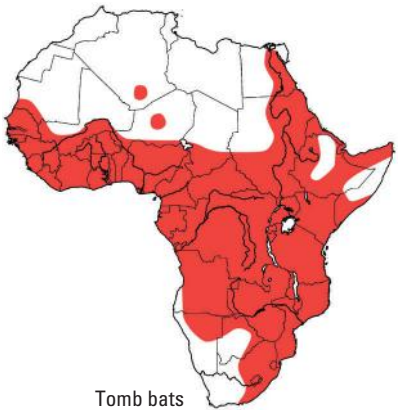
African Sheath-tailed Bat

AFRICAN SHEATH-TAILED BAT *Coleura afra*

MEASUREMENTS HB 52–66mm. FA 44–53mm. W 7–10g.
RECOGNITION A small sooty-brown bat with exaggerated head-up posture and unusually vertical tail. The ear tragus has a pimple on the outer edge. The nostrils overhang the lower jaw.
HABITAT Ranges through savannas and woodlands in Africa and Arabia. Roosts in caves, houses and on rocky outcrops, especially close to open water.
FOOD Very small insects that may occasion seasonal migrations.
STATUS An extremely sensitive species that dies rapidly after capture. Widespread but numbers and presence are erratic in any one locality.

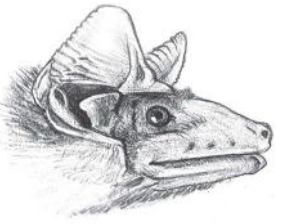
TOMB BATS *Taphozous*

MEASUREMENTS HB 70–93mm. FA 58–70mm. W 20–30g.
RECOGNITION Typical sheath-tailed bats with a skin pocket below the wrist (which can produce a whirring sound) and a concavity behind the swollen, tubular muzzle. Tomb bats are alert while roosting but unwilling to fly if disturbed and will scurry sideways along vertical walls or trunks. They roost in spaced groupings and mark their stations with greasy smears from the throat sacs.
SPECIES *T. mauritianus* (sub-Saharan Africa and Indian Ocean islands), *T. perforatus* (Africa, NW India), *T. nudiventris* (Sahelian and E Africa to Burma), *T. hildegardeae* (East Africa), *T. hamiltoni* (upper Nile valley, Chad).



Tomb bats

T. nudiventris



T. hildegardeae

T. perforatus

T. nudiventris

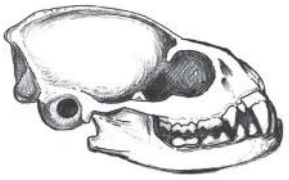
T. mauritianus

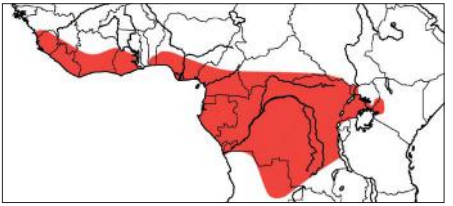
T. mauritianus

HABITAT From arid to wooded habitats in subtropical Africa and south Asia. Tomb bats acquired their name as a result of their favouring roosting sites among the ancient monuments of Egypt. They may roost singly or in dense colonies.
FOOD Mainly moths hunted along habitual flight-paths.
STATUS This genus includes both widely distributed and more localised species.

BLACK-HAWK BAT *Saccolaimus peli*

OTHER NAMES Pel's Pouched Bat, Giant Pouched Bat.
MEASUREMENTS HB 110–157mm. FA 84–97mm. W 77–114g.
RECOGNITION A very large black bat with broad, flat head and shoulders, large eyes, small ears and short, greasy fur. Both sexes have a throat sac. Wings are pointed and flight is falcon-like. Often visible over forest clearings just before nightfall.
HABITAT Rainforests from Sierra Leone to W Kenya.
FOOD Beetles and other high-flying insects caught above the canopy and along the margins of high forest. Very active and acrobatic while feeding, making an audible 'chuwee' call.
STATUS A conspicuous rainforest species, widely distributed but apparently at low densities.





Black-hawk Bat

FREE-TAILED BATS MOLOSSIDAE

Guano bats	*Tadarida* (5 species)
Wrinkle-lipped bats	*Chaerophon* (10 species)
Mops free-tailed bats	*Mops* (12 species)
Winged-mouse bats	*Myopterus* (2 species)
Flat-headed bats	*Mormopterus* (2 species)
East African Flat-headed Bat	*Platymops setiger*
Roberts's Flat-headed Bat	*Sauromys petrophilus*
Giant Mastiff Bat	*Otomops martiensseni*

Bats of this family are easily identifiable by their tails, which are free beyond a narrow membrane, and by the crumpled lips, large nostrils and joined-up ears. They have short, stout feet with muscular legs and long, narrow wings. They are fast, long-distance fliers. All species are strong-smelling and possess scent-dispensing 'brushes' of specialised hairs on their outer toes. Distribution is worldwide at tropical latitudes.

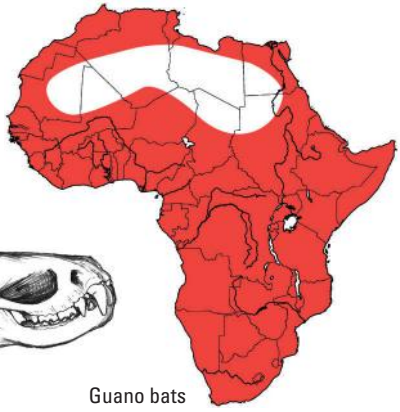
Tadarine bats are presented here as three genera: *Tadarida*, *Chaerophon* and *Mops*. These are sometimes treated as subgenera of *Tadarida*, and sometimes united in a single multi-species *Tadarida*. Traditional diagnoses for each tadarine grouping remain tentative and provisional until comprehensive genetic analyses are available. Shape of ear and upper third molar are diagnostic (see below).

Tadarida *Chaerophon* *Mops*

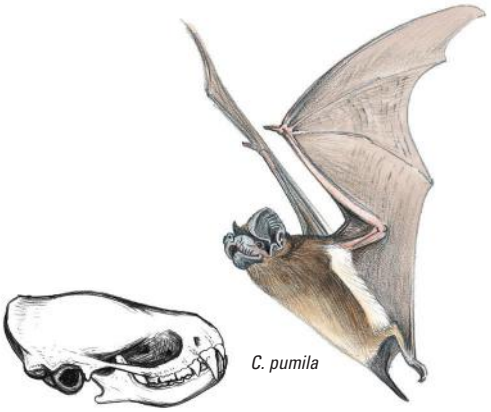
GUANO BATS *Tadarida*

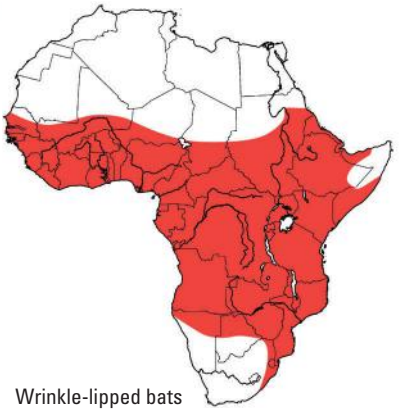
MEASUREMENTS HB 61–102mm. FA 42–67mm. W 9–55g.
RECOGNITION Free-tailed bats with large 'square' ears that meet but are not quite joined across the nose. They have large margins to the palate and the third molar is not reduced.
SPECIES *T. aegyptiaca*, *T. lobata*, *T. fulminans*, *T. teniotis*, *T. ventralis*.
HABITAT All habitats, predominantly in Africa but also in Central America and S Asia.
FOOD Insects.
STATUS Most species well distributed. Some are very common.

T. aegyptiaca



Guano bats



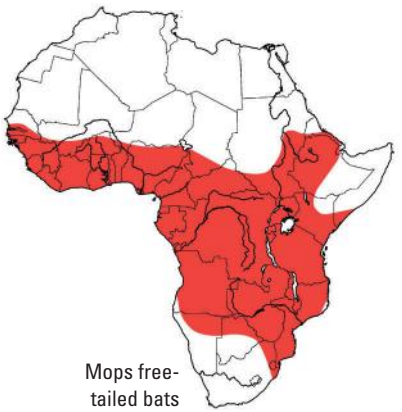

Wrinkle-lipped bats

WRINKLE-LIPPED BATS *Chaerophon*

MEASUREMENTS HB 45–86mm. FA 32–53mm. W 7–38g.
RECOGNITION Free-tailed bats with large ears joined above the bridge of the nose. The tuft of fur on the forehead is very long in some species. The skull is slightly flattened. Strong-smelling bats with an audible call not unlike the screaming of swifts in muted form.
SPECIES *C. pumila*, *C. aloysiisabaudiae*, *C. ansorgei*, *C. bemmeleni*, *C. bivittata*, *C. chapini*, *C. gallagheri*, *C. major*, *C. nigeriae*, *C. russata*.
HABITAT Diverse distribution in various vegetation zones. *C. pumila* is found all over sub-Saharan Africa, Madagascar and S Arabia.
FOOD Variety of small flying insects.
STATUS Most species common or widespread.

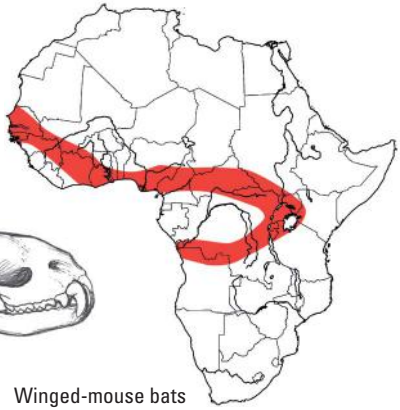
MOPS FREE-TAILED BATS *Mops*

MEASUREMENTS HB 56–94mm. FA 27–67mm. 6–69g.
RECOGNITION Free-tailed bats with the ears joined over the forehead (exposing the muzzle and nostrils). The third molar is reduced to a V-shape. Compact, robust and very variable in colour. The most 'derived' form of free-tailed bats. They emit sharp, audible clicks and like to fly in 'flocks'.
SPECIES *M. condylura*, *M. brachypterus*, *M. congicus*, *M. demonstrator*, *M. midas*, *M. nanulus*, *M. niangarae*, *M. niveiventer*, *M. petersoni*, *M. spurreli*, *M. thersites*, *M. trevori*.
HABITAT Forests, woodlands and savannas. Some species migrate, even in great flocks. Some roost in small numbers, others in hundreds, in houses, caves, hollows and, occasionally, in shady vegetation.
FOOD Small flying insects.
STATUS Most species common.


Mops free-tailed bats

M. midas

M. whitleyi

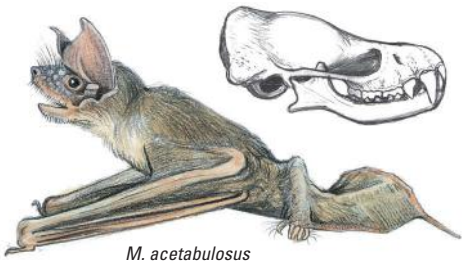


Winged-mouse bats

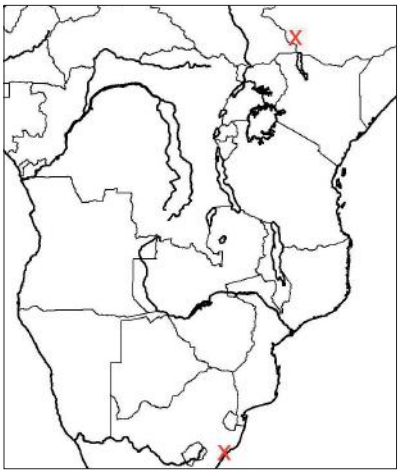
WINGED-MOUSE BATS *Myopterus*

MEASUREMENTS HB 53–76mm. FA 35–54mm. W 10–22g.
RECOGNITION Free-tailed bats with widely separated ears, large tragi, pale wings and a greatly reduced third molar. Lips are unwrinkled but bristly along their upper margins. The nose is smooth, rounded and supposedly rat-like.
SPECIES *M. whitleyi* (forest zone from Ghana to Uganda), *M. daubentonii* (Senegal to NE DR Congo).
HABITAT Forest and forest–savanna mosaics. Solitary, roosting in vegetation or in trunk crevices.
FOOD Insects.
STATUS Poorly known.

M. francoismoutoui



M. acetabulosus



Flat-headed bats

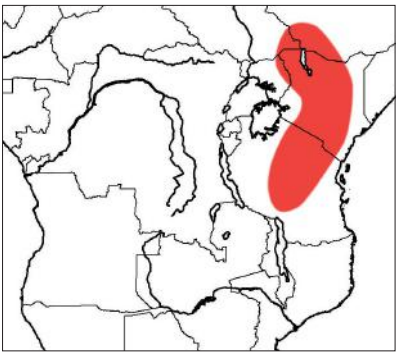
FLAT-HEADED BATS *Mormopterus*

OTHER NAMES Little mastiff bats.
MEASUREMENTS HB 49–52mm. FA 38–43mm. W 5.0–8.2g.
RECOGNITION Small, free-tailed bats with 'warty' muzzles and a main 'brush' of bristles above the nose. The head and body are flattened, the tail long, and ears pointed and separate. The third molar is not reduced. Skulls resemble *Sauromys*.
SPECIES *M. acetabulosus*, *M. francoismoutoui*.
HABITAT Far-ranging tropical bats, commonest on Indian Ocean islands (especially Madagascar). Possibly vagrants on continental Africa.
FOOD Insects.
STATUS Poorly known.

EAST AFRICAN FLAT-HEADED BAT *Platymops setiger*

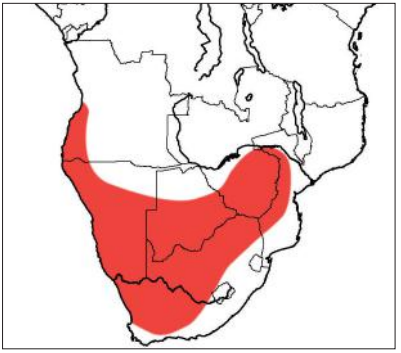
OTHER NAMES Peters's Flat-headed Bat.
MEASUREMENTS HB 50–78mm. FA 27–36mm. W 7–18g.
RECOGNITION A very flat, free-tailed bat with a distinct, very dense 'moustache' of strong, forwardly directed bristles under the nose. Forearms are very 'warty'. Ears are blunt and laterally

East African Flat-headed Bat



East African Flat-headed Bat

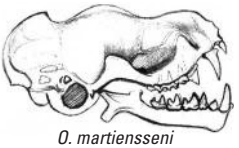
oriented. Small colonies roost in narrow horizontal crevices in rock outcrops and cliffs which are characteristically very strong smelling.
HABITAT Dry, rocky habitats at various altitudes in NE Africa.
FOOD Small beetles and other insects.
STATUS Poorly known.



Roberts's Flat-headed Bat

ROBERTS'S FLAT-HEADED BAT *Sauromys petrophilus*

MEASUREMENTS HB 60–82mm. FA 37–50mm. W 6–22g.
RECOGNITION Resembles *Platymops* in extreme flattening of body and head (to fit in narrow crevices). Simple ears separated by narrow gap. Upper lip smooth with a few stout, short hairs.
HABITAT Rocky outcrops, mainly south of Zambezi R.
FOOD Beetles, moths and other mainly hard-shelled insects.
STATUS Patchily but widely distributed in southern Africa.

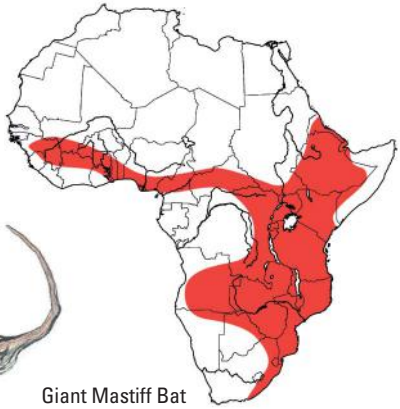


O. martiensseni

GIANT MASTIFF BAT *Otomops martiensseni*

MEASUREMENTS HB 88–109mm. FA 61–74mm. W 26–47g.
RECOGNITION A large, free-tailed bat with very long ears attached along the whole length of the head and very long, streamlined proportions. The upper lip has flanges. Notable for a circular pocket gland on the throat. Wings are long, narrow and pointed. Flight is fast and high.
HABITAT African representative of a pan-tropical group of very successful bats hunting high above all ecotypes and at a range of altitudes. Congregates in tens of thousands in breeding caves which

are vacated en masse on a seasonal or periodic basis.
FOOD Beetles and large insects caught high above ground (or over water).
STATUS Widespread and common but vulnerable as it is concentrated in a few caves.



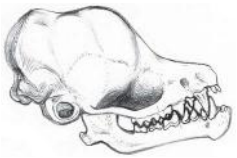
Giant Mastiff Bat

LONG-FINGERED BATS MINIOPTERIDAE

By tradition, long-fingered bats were attached to Vespertilionidae. Separate family status had been proposed in 1977: now just such elevation has been supported by molecular phylogenetics estimating that this family has been a separate lineage for some 43-46 million years. New genetic profiles suggest distant affinity to the Molossidae and to the South American Natalidae as well as to Vespertilionidae. This family numbers some 19 species worldwide, but is very poorly known in Africa where six, perhaps seven species occur. The greatly elongated fingers and unique folding pattern of the digit tips are easily seen diagnostic details.

LONG-FINGERED BATS *Miniopterus*

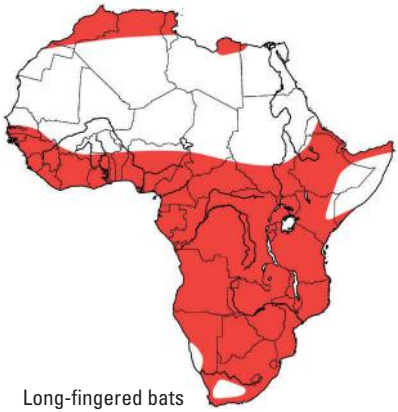
MEASUREMENTS HB 48–66mm. FA 37–52mm. W 3–19g.
RECOGNITION Double folding of the wing digits (which are exceptionally long) is a very distinctive feature. These big-brained bats have a high-domed cranium, a very small, pointed muzzle and are dark in colour. Roost in large numbers deep in caves and at least some are migratory.
SPECIES *M. schriebersi*, *M. fraterculus*, *M. inflatus*, *M. africanus*, *M. minor*, *M. natalensis*.
HABITAT Very varied habitats in Africa, Eurasia and Australia.
FOOD Insects.



M. schriebersi

double-folded digits, ventral view

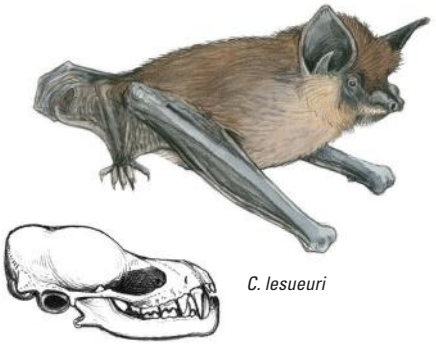
M. schriebersi

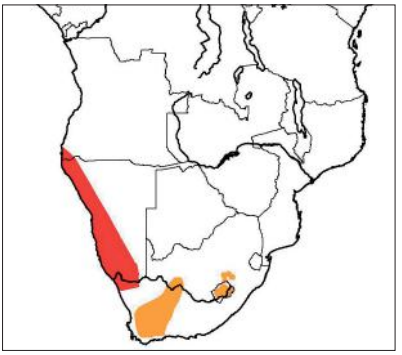


Long-fingered bats

PIMPLE-WINGED BATS CISTUGIDAE

The dentition of the two *Cistugo* species resembles *Myotis*, in which these species were included until recent genetics demonstrated that *Cistugo* may represent a lineage that actually preceded the emergence of *Myotis* and the vespertilionids – in other words, a very ancient ancestral type of bat for which some taxonomists have proposed familial status – Cistugidae.





PIMPLE-WINGED BATS *Cistugo*

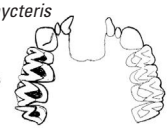
OTHER NAMES Wing-gland bats.
MEASUREMENTS HB 40–55mm. FA 32–38mm. W 5.5–8g.
RECOGNITION *Cistugo* have one or two pimple-like glands on the web of each wing.
SPECIES *C. lesueuri, C. seabrae.*
HABITAT South-west African desert and Karoo region, usually near open water.
FOOD Insects caught on the wing or snatched off leaves.
STATUS Genetically, the most conservative of all vespertilionid-like bats. Little known and specific status of *lesueuri* tentative.

VESPER BATS VESPERTILIONIDAE

Hairy bats	*Myotis* (11 species)
Woolly bats	*Kerivoula* (7 species)
House bats	*Scotophilus* (6 species)
Evening bats	*Scotoecus* (2 species)
Schlieffen's Twilight Bat	*Nycticeinops schlieffeni*
Long-eared bats	*Plecotus* (3 species)
Hemprich's Long-eared Bat	*Otonycteris hemprichii*
Barbastelle bats	*Barbastella* (2 species)
Butterfly bats	*Glauconycteris* (11 species)
Badger Bat	*Niumbaha superba*
Tropical long-eared bats	*Laephotis* (4 species)
Serotine bats	*Eptesicus* (5 species)
Moloney's Flat-headed Bat	*Mimetillus moloneyi*
Noctules	*Nyctalus* (2 species)
Pipistrelles	*Pipistrellus* (29 species)

Vesper bats are a very large and successful family of simple-nosed bats. At a casual glance most vesper bats look bewilderingly alike. Dental patterns and skull structures must be examined closely

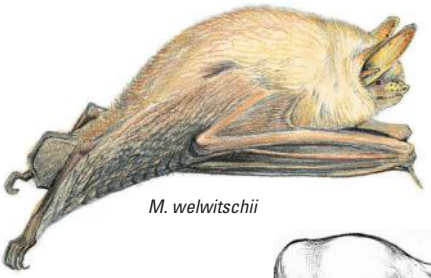
Key to Vespertilionids

	LOWER JAW	SKULL PROFILE	HEAD	TOOTH FORMULA
Myotis				$\frac{2\text{-}1\text{-}3\text{-}3}{3\text{-}1\text{-}3\text{-}3} = 38$ 11 species profile on p.353
Laephotis				$\frac{2\text{-}1\text{-}3\text{-}3}{3\text{-}1\text{-}2\text{-}3} = 32$ 4 species profile on p.357
Glauconycteris				$\frac{2\text{-}1\text{-}1\text{-}3}{3\text{-}1\text{-}2\text{-}3} = 32$ 11 species profile on p.356
Kerivoula				$\frac{2\text{-}1\text{-}3\text{-}3}{3\text{-}1\text{-}3\text{-}3} = 38$ 7 species profile on p.353
Pipistrellus				$\frac{2\text{-}1\text{-}2\text{-}3}{3\text{-}1\text{-}2\text{-}3} = 34$ 28 species profile on p.359
Eptesicus				$\frac{2\text{-}1\text{-}1\text{-}3}{3\text{-}1\text{-}2\text{-}3} = 32$ 5 species profile on p.358
Mimetillus				$\frac{2\text{-}1\text{-}1\text{-}3}{3\text{-}1\text{-}2\text{-}3} = 32$ note very short wing 1 species profile on p.358
Nycticeinops				$\frac{1\text{-}1\text{-}1\text{-}3}{3\text{-}1\text{-}2\text{-}3} = 30$ or $\frac{1\text{-}1\text{-}2\text{-}3}{3\text{-}1\text{-}2\text{-}3} = 32$ 1 species profile on p.355
Scotophilus				$\frac{1\text{-}1\text{-}1\text{-}3}{3\text{-}1\text{-}2\text{-}3} = 30$ 2 species profile on p.354

in order to distinguish some genera and species. The most obvious characteristics of this family are small eyes, separate ears, with noticeable tragi, and long tails enclosed in membrane. Most species have glands on the muzzle (which may periodically swell or shrink in size).

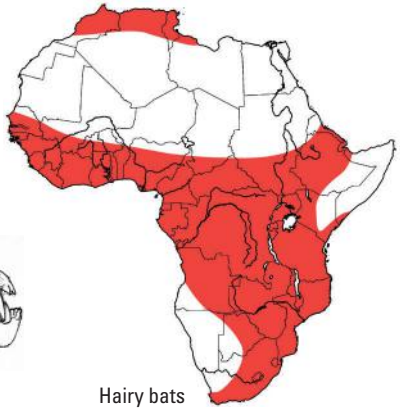
Primitive bat dentition is characterised by 38 teeth (2-1-3-3:3-1-3-3) set in a long, slender snout. This formula occurs in pimple-winged bats, *Cistugo* and hairy bats, *Myotis*. Genetically, the former is thought to represent the last survivors of a lineage that preceded the emergence of the Vespertilionidae. Family status, Cistugidae, has been proposed, but on gross morphological criteria *Cistugo* and *Myotis* resemble sibling genera (so the two genera and families are placed in close conjunction here) even as their familial distinctness is acknowledged. Long-fingered bats, *Miniopterus*, until recently another vesper genus, have also been found to genetically pre-date the emergence of Vespertilionidae and now have their own family, Miniopteridae.

Pipistrelles are thought to have derived from a *Myotis*-like stem. In the more advanced genera faces are shorter and the teeth have become reduced in number (see key). Vesper bats have a world-wide distribution and occupy all but the very coldest regions and habitats.



M. welwitschii

M. bocagei



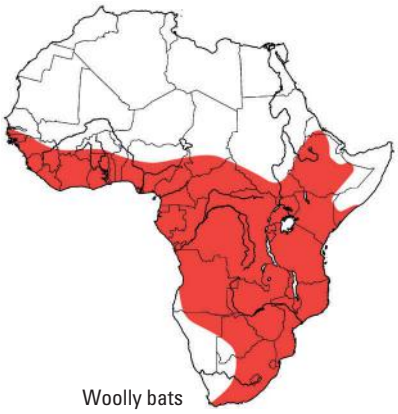
Hairy bats

HAIRY BATS *Myotis*

OTHER NAMES Mouse-eared bats.
MEASUREMENTS HB 42–77mm. FA 33–65mm. W 5–33g.
RECOGNITION Small bats with long, hairy muzzles and narrow ears with spike-shaped tragi. The numerous teeth have sharp, pointed cusps (see key for tooth formula). They seldom roost in houses, preferring hollow trees, deep caves or vegetation.
SPECIES *M. bocagei*, *M. capaccinii*, *M. deiteri*, *M. emarginatus*, *M. morrisi*, *M. mystacinus*, *M. nattereri*, *M. punicus*, *M. scotti*, *M. tricolor*, *M. welwitschii*.
HABITAT A wide range of vegetation types and altitudes. Some species may be scattered, roosting singly or in small groups, while others form larger colonies.
FOOD Small insects caught in slow flight within 5m of the ground.
STATUS Many species are very poorly known.

WOOLLY BATS *Kerivoula*

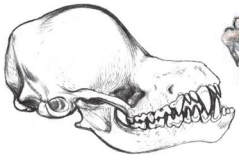
MEASUREMENTS HB 31–50mm. FA 25–39mm. W 2.2–10.5g.
RECOGNITION The woolly fur has a frizzled, frosted or 'crinkly' appearance. The funnel-shaped ears have a long, pointed tragus. The long, sharp muzzle and domed cranium are generally concealed by dense fur, as are the minute eyes. The membrane bears a fine fringe of short hair. Roost among dead leaves, in lichen, old bird's nests, thatch or hollow branches.



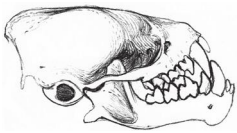
Woolly bats

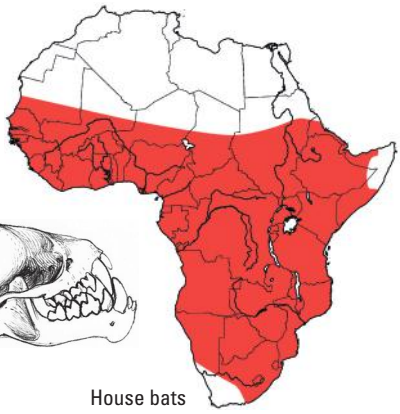
SPECIES *K. africana*, *K. argentata*, *K. cuprosa*, *K. eriophora*, *K. lanosa*, *K. phalaena*, *K. smithi*.
HABITAT Well-watered but otherwise diverse habitats. Woolly bats emerge late and retire early.
FOOD Very small insects caught at low levels in slow, dancing flight.
STATUS Poorly known.

K. argentata



S. nigrita





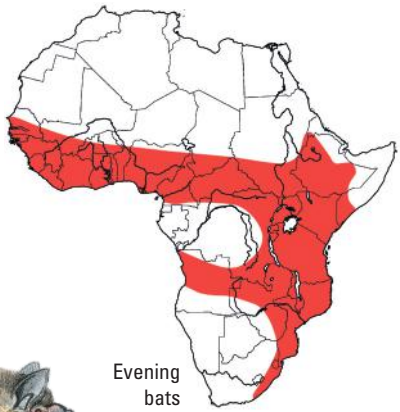
House bats

HOUSE BATS *Scotophilus*

MEASUREMENTS HB 71–103mm. FA 41–88mm. W 12–91g.
RECOGNITION Robust bats with blunt heads and long, tapering tragi. There are swollen glands in the corner of the mouth. Posterior teeth are greatly reduced. Colouring varies from greenish olive and yellow to dark brown and off-white. Emerge early and take fast, sweeping flights along habitual flyways.
SPECIES *S. dinganii*, *S. leucogaster*, *S. nigrita*, *S. nucella*, *S. nux*, *S. viridis*.
HABITAT Very varied ecotypes, including uplands, forests and scrub-desert in Africa and Asia.
FOOD Hard-bodied insects.
STATUS Poorly known but very widespread.

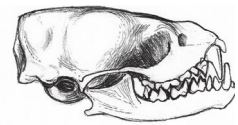
EVENING BATS *Scotoecus*

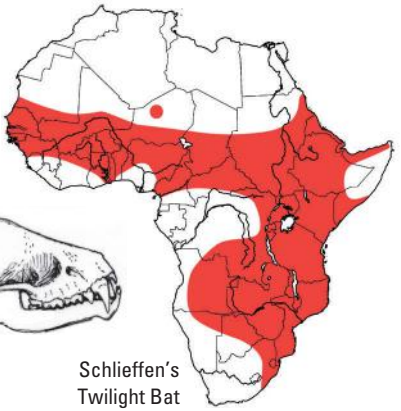
OTHER NAMES Lesser house bats.
MEASUREMENTS HB 49–60mm. FA 29–40mm. 5–15g.
RECOGNITION Broad-faced brown bats with a blunt tragus in the round ears. Teeth are robust, the canines flat-fronted. Males have an exceptionally long penis. Variable in colour.
SPECIES *S. hirundo*: dark-winged. *S. albofuscus*: pale-winged.
HABITAT Tropical bats inhabiting woodlands, savannas and dry *Acacia* country.
FOOD Insects.
STATUS Poorly known.



Evening bats

S. hirundo





Schlieffen's Twilight Bat

SCHLIEFFEN'S TWILIGHT BAT

Nycticeinops schlieffeni

MEASUREMENTS HB 37–48mm. FA 28–35mm. W 4–9g.

RECOGNITION A variably coloured bat with dark membranes and a bare, swollen muzzle. The triangular ear has a very narrow, pointed tragus. Emerges early and has an erratic flight. Roosts alone in crevices in trees and buildings.

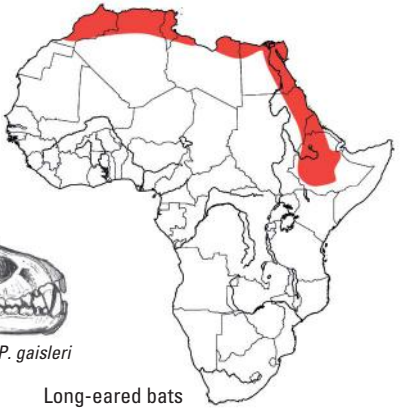
HABITAT Very widespread in savannas and relatively arid habitats in Africa and Arabia.

FOOD Small insects.

STATUS Common and widespread.

P. christii

P. gaisleri



Long-eared bats

LONG-EARED BATS

Plecotus

MEASUREMENTS HB 42–55mm. FA 36–42mm. W 6.5–10g.

RECOGNITION Very long-eared, woolly bats with large, tapered tragi and a blunt face. The long fur has a dark base and grey-brown surface tints. Claws and feet are small. They chirp or hum if disturbed.

SPECIES *P. balensis* (Ethiopian highlands), *P. christii* (Egypt, N Sudan), *P. gaisleri* (Morocco – Libya).

HABITAT Dry, open Mediterranean landscapes, especially warm valleys. Roost alone or in twos and threes in caves, mines (winter) or buildings.

FOOD Moths, beetles and other insects taken off foliage or in flight.

STATUS Peripheral range in N and NE Africa. Main distribution in Europe.

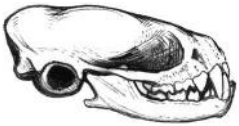
HEMPRICH'S LONG-EARED BAT

Otonycteris hemprichii

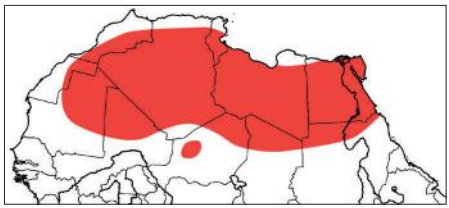
OTHER NAMES Hemprich's Desert Bat.

MEASUREMENTS HB 67–87mm. FA 50–65mm. W 18–19g.

RECOGNITION A large-eared, long-headed desert bat with long, silky pale fur and semi-translucent



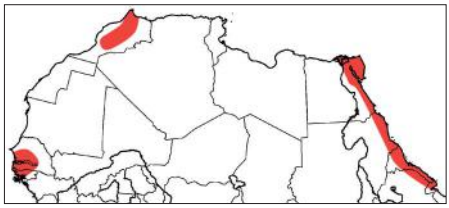
Hemprich's Long-eared Bat



Hemprich's Long-eared Bat

membranes. Flight is slow and erratic. Emits a buzz call when disturbed in roost.
HABITAT Desert and subdesert steppe environments, roosting in rock crevices, cliffs or buildings.
FOOD Desert insects.
STATUS Widespread but poorly known.

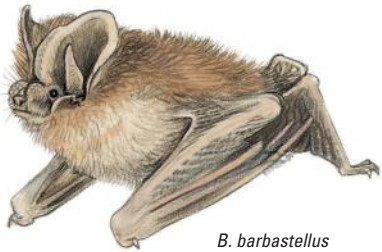
B. barbastellus



Barbastelle bats

BARBASTELLE BATS *Barbastella*

MEASUREMENTS HB 52–74mm. FA 36–44mm. W 7–8g.
RECOGNITION Very dark bats with blunt noses and upward-facing nostrils. The forward edges of the large, emarginated ears join forward of the eyes to give a very pinched, pug-nosed appearance. The tragus is triangular. All naked skin is black or deep brown. Form small summer groups of 10–100 but roost in larger numbers in winter. Utter audible chirps and hums.
SPECIES *B. barbastellus* (Morocco to Senegal), *B. leucomelas* (Egypt).
HABITAT Dry, open woodlands and temperate mountains. Occasional migrants; known to travel nearly 300km.
FOOD Small, soft insects often caught over water or off foliage in slow but well-controlled flight.
STATUS A marginal species for Africa.

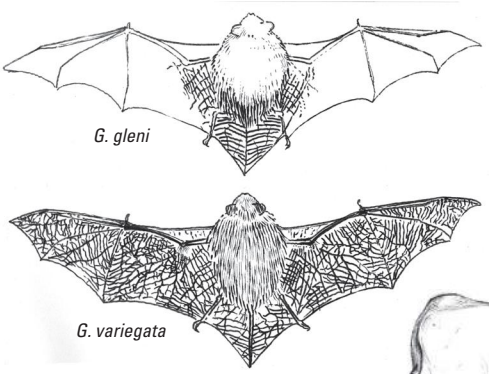


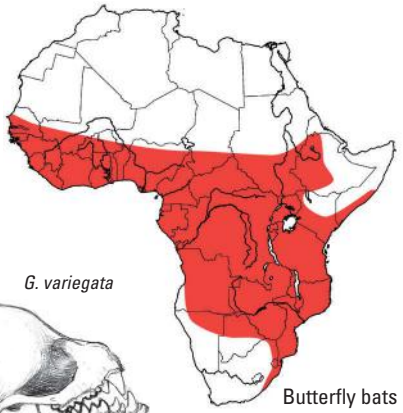
B. barbastellus

BUTTERFLY BATS *Glauconycteris*

MEASUREMENTS HB 43–63mm. FA 32–48mm. W 4–19g.
RECOGNITION Small, furry bats with marked wings, broad, blunt faces with widely spaced nostrils, and rounded ears that flare out from the corners of the mouth and are connected by a cheek lobe below bluntly hooked tragi. Often reluctant to fly from their day-perches, merely half opening their wings. Roost in trees or buildings, often attracted to lights, and make audible squeaks.
SPECIES *G. alboguttata*, *G. argentata*, *G. beatrix*, *G. curryae*, *G. egeria*, *G. gleni*, *G. humeralis*, *G. kenyacola*, *G. machadoi*, *G. poensis*, *G. variegata*.
HABITAT Woodlands, forests and moist savannas. May roost in clusters under the shelter of large leaves or in thatch.
FOOD Moths and other small, soft-bodied insects caught in flight early in the evening.
STATUS Poorly known.

G. argentata



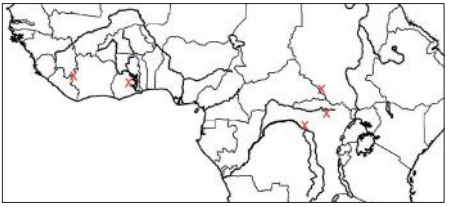

Butterfly bats

BADGER BAT *Niumbaha superba*

OTHER NAMES Pied Butterfly Bat.
MEASUREMENTS HB 49–63mm. FA 45–48mm. W (est.) 14g.
RECOGNITION A newly described genus extracted from *Glauconycteris* to accommodate a species (possibly a lineage) of particularly robust butterfly bats with brilliantly piebald contrasting pelage patterns.
HABITAT Semi-deciduous forest and lowland rainforest.
FOOD Not known.
STATUS The few known specimens come from several widely distant localities.

Badger Bat

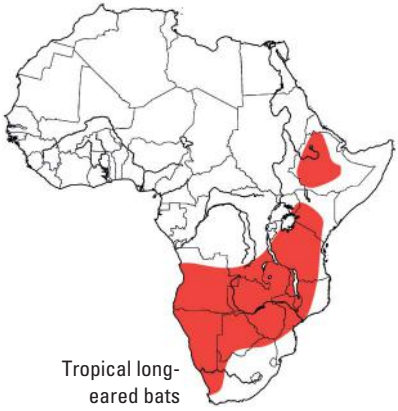
Badger Bat


Badger Bat

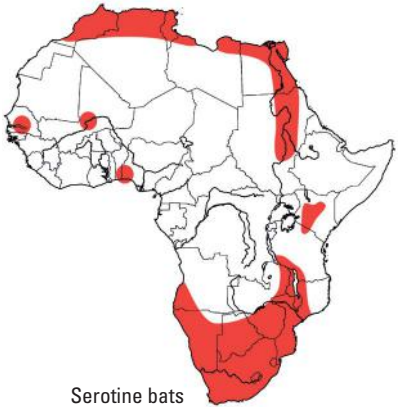
TROPICAL LONG-EARED BATS *Laephotis*

MEASUREMENTS HB 46–65mm. FA 30–41mm. W 5–11g.
RECOGNITION The long ears have very large, curved tragi. These bats have a short face, long pale fur and a light underside. Roost in day-time under dead bark.
SPECIES *L. angolensis*, *L. botswanae*, *L. namibensis*, *L. wintoni*.
HABITAT Rare bats found in dry woodlands and savannas of southern and East Africa. *L. wintoni* has the widest distribution.
FOOD Insects.
STATUS Poorly known.
See map on p.358.

L. wintoni



Tropical long-eared bats



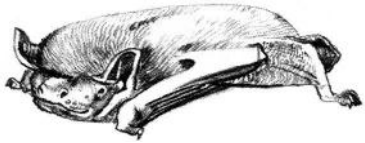
Serotine bats

SEROTINE BATS *Eptesicus*

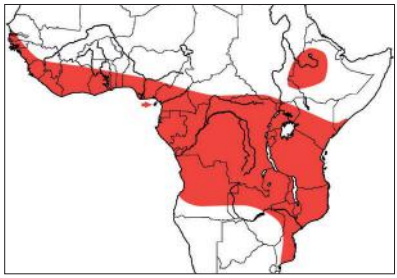
E. hottentotus

MEASUREMENTS HB 45–77mm. FA 34–54mm. W 10–27g.
RECOGNITION Serotine bats are distinguished by their relatively short ears and blunt tragi and the almost flat top to their skulls. They resemble pipistrelles but have only one upper incisor. Their flight also resembles that of pipistrelles: erratic fluttering punctuated by fast swoops and dives. The wings keep relatively constant profile in flight and the tail membrane appears blunt and rounded. They may make audible clicks as they fly.
SPECIES *E. bottae*, *E. floweri*, *E. hottentotus*, *E. platyops*, *E. serotinus*.
HABITAT Both forest and non-forest species, low and high fliers, roosting in vegetation, caves and houses.
FOOD Small insects caught in flight.
STATUS Poorly known.

MOLONEY'S FLAT-HEADED BAT *Mimetillus moloneyi*



OTHER NAMES Moloney's Mimic Bat.
MEASUREMENTS HB 51–63mm. FA 27–31mm. W 5.5–10g.
RECOGNITION Easily recognised in the air by its fast, short-winged, whirring flight; very direct with no sharp turns. Head and body are flattened and forearms and wings are short and compact. It is dark brown all over, with short, greasy fur, and has very large glands on the frog-like muzzle.
HABITAT Forest and moist forest–savanna mosaics in equatorial Africa, roosting under bark.
FOOD Flying termites and ants.
STATUS Widespread and common but never in large numbers.



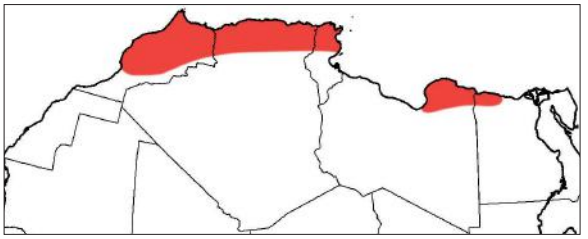
Moloney's Flat-headed Bat

Moloney's Flat-headed Bat

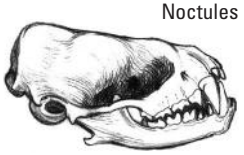
N. leisleri

NOCTULES *Nyctalus*

MEASUREMENTS HB 60–90mm. FA 41–64mm. W 11–58g.
RECOGNITION Brown pug-nosed bats with dark membranes and long, narrow wings. The fur extends from the body onto the membranes, both above and below. Flight is fast, on angled wings. The metallic calls are very audible.
SPECIES *N. lasiopterus*, *N. leisleri*.
HABITAT Temperate and migratory bats with marginal extensions of range into N Africa.
FOOD Large insects.
STATUS Marginal species; *N. lasiopterus* very rare everywhere.



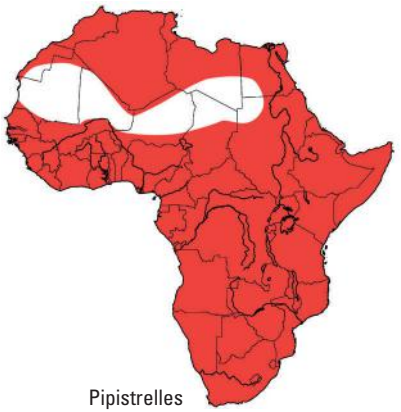
Noctules



N. lasiopterus

PIPISTRELLES *Pipistrellus*

MEASUREMENTS HB 39–57mm. FA 22–39mm. W 3.5–10.5g.
RECOGNITION Very small bats of variable colouring. Prominent nostrils bring the nose to a sharp point behind the swollen muzzle. Dental formula is 2-1-2-3:3-1-2-3 = 34. The tragus shape is distinctive for most species. Genetic studies suggest that some pipistrelles have closer affiliations, or may belong to other genera (notably *Neoromicia*, a genus not listed in this edition of the guide). Flight is fluttering, with frequent angular turns and swoops.
SPECIES *P. aero*, *P. anchietai*, *P. ariel*, *P. brunneus*, *P. capensis*, *P. crassulus*, *P. deserti*, *P. eisentrauti*, *P. grandidieri*, *P. guineensis*, *P. hanaki*, *P. helios*, *P. hesperidus*, *P. inexpectatus*, *P. kuhlii*, *P. melckorum*, *P. musciculus*, *P. nanulus*, *P. nanus*, *P. permixtus*, *P. pipistrellus*, *P. rendalli*, *P. rueppellii*, *P. rusticus*, *P. savii*, *P. somalicus*, *P. tenuipinnis*, *P. zuluensis*.
HABITAT All habitats.
FOOD Insects.
STATUS Too many species, too poorly known to assess.



Pipistrelles

P. nanus

CARNIVORES CARNIVORA

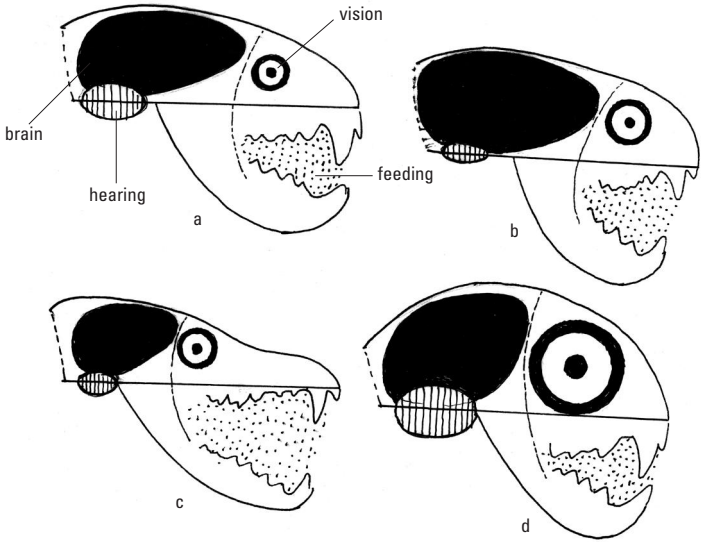
Dogs and allies	Canidae
Mustelids	Mustelidae
Fur seals	Otariidae
True seals	Phocidae
Tree Civet	Nandiniidae
Cats	Felidae
Genets and civets	Viverridae
Hyaenids	Hyaenidae
Mongooses	Herpestidae

RECOGNITION The carnivores are a group of mainly 'animal-eaters', ranging from weasels (75g) to the Lion (270kg), the dog to the cat. All share 'carnassial', or slicing, teeth (fourth upper against fifth lower cheek-teeth), although the shapes of these teeth are greatly modified in some species. Modern carnivores are split into two suborders, the caniforms and feliforms, bringing a domestic, hearthside familiarity to an important scientific debate – how come cats and dogs?

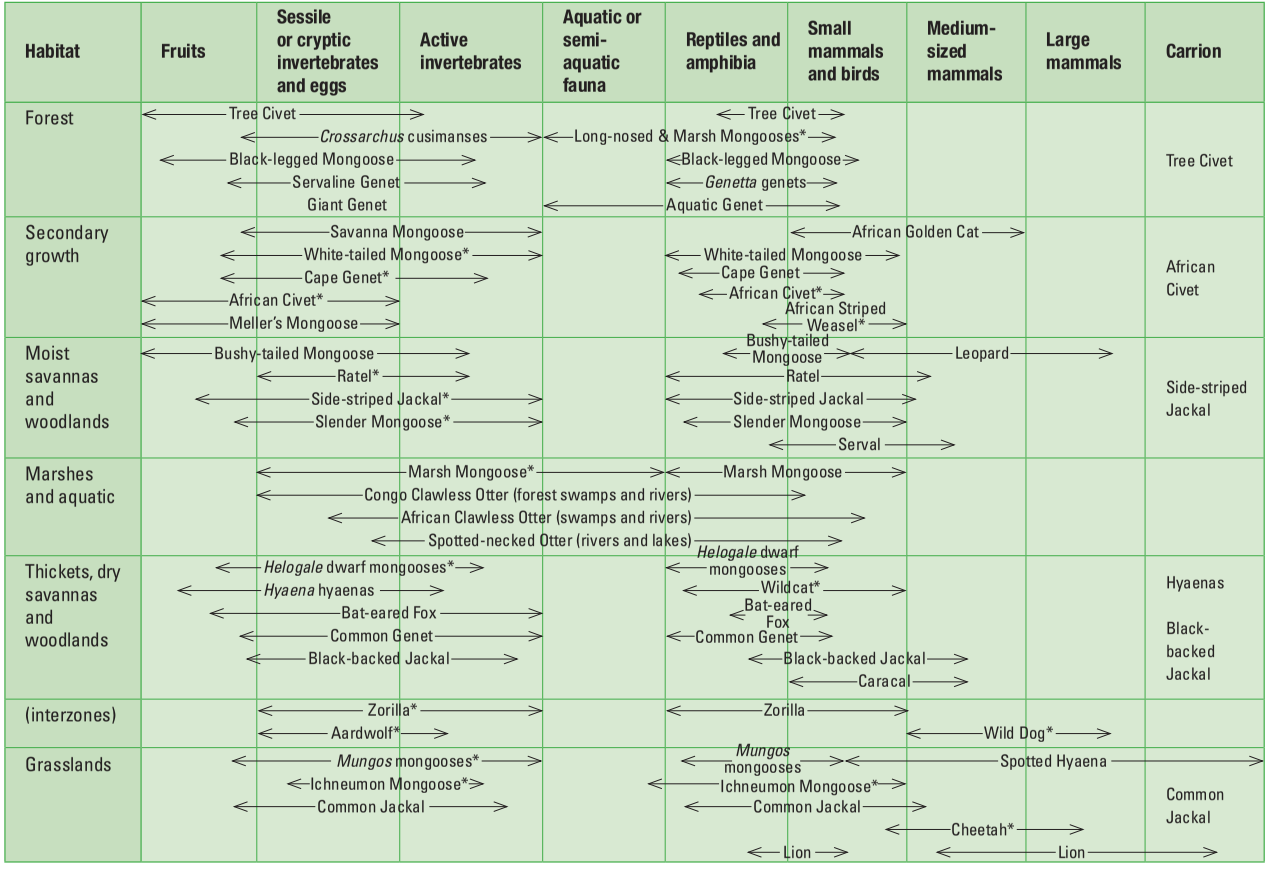
GENEALOGY For many years it was widely thought that all surviving carnivores derived from miacoids, fossils of which are abundant (but only *outside* Africa) and dated to 60–50 mya. This supposition was reinforced by some of these generalised carnivores resembling extant types, such as the civets. Contemporary studies that have combined genetic and fossil data have disproved this long-established inference by showing that miacoids were unrelated to the common ancestor of all extant carnivores.

One important corollary is that the evolution of modern carnivores was later and faster than was formerly thought, and the split between dog and cat ancestors advances from over 60 mya to about 43 mya!

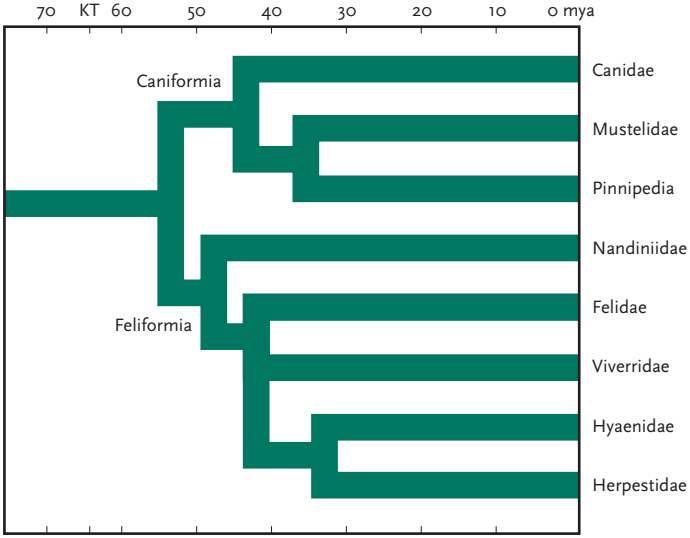
Another essentially modern insight is that the ancestors of all carnivores immigrated into Africa. Some are so recent that they are still conspecific with Eurasian populations (Red Foxes, Common Weasels and others) but others, such as mongooses, Herpestidae, radiated within Africa, as did the hyaenas. Mustelids, instead, are carnivores adapted to northern temperate climates but a few



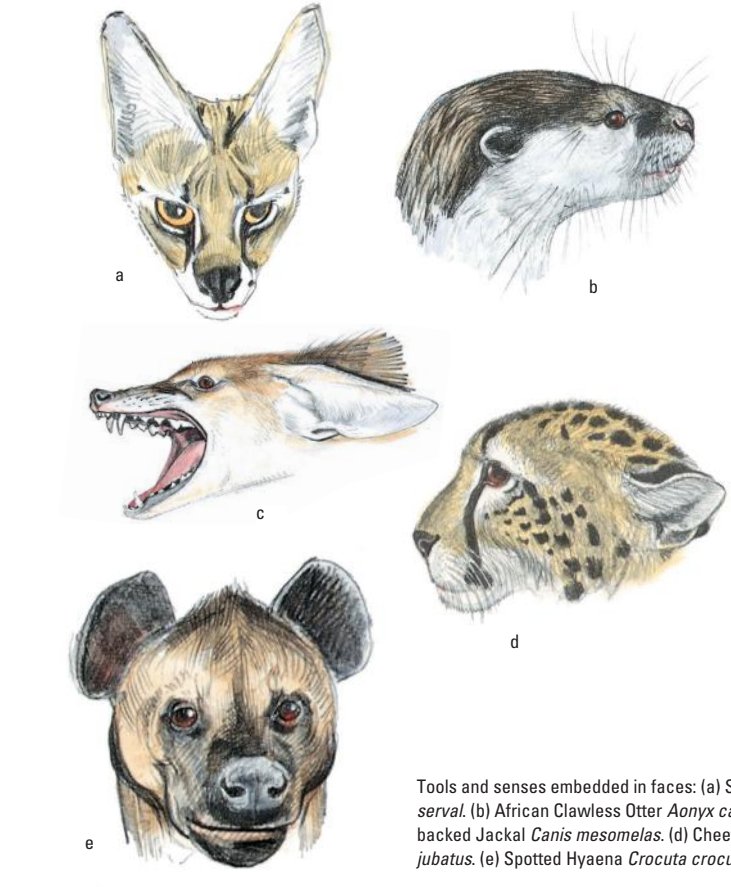
Relative sizes of capsules enclosing specific activities in carnivore skulls. (a) Herpestid (*Atilax*). (b) Mustelid (*Poecilogale*). (c) Canid (*Canis simensis*). (d) Felid (*Felis nigripes*).



Carnivore niches. * Species thus marked occupy a wider range of habitats than can be suggested in a simplified table.



Tentative phylogenetic tree for extant African carnivora (after Flynn *et al.* 2005, Eizerik & Murphy 2009).



Tools and senses embedded in faces: (a) Serval *Leptailurus serval*. (b) African Clawless Otter *Aonyx capensis*. (c) Black-backed Jackal *Canis mesomelas*. (d) Cheetah *Acinonyx jubatus*. (e) Spotted Hyaena *Crocuta crocuta*.

specialised forms have become established and even speciated in Africa. The dog family originated in North America and has become very widespread and successful. The origins of the cat family are probably Asian.

ECOLOGY Carnivores are well distributed throughout the many ecosystems of Africa and the chart below summarises the separation of species according to habitat and diet.

NATURAL HISTORY The number and diversity of carnivores is one of the surest signs of ecological richness because each species sits at the top of a different food chain belonging to a different cycle of organic matter. Each type of carnivore therefore implies a much larger ecological community. Most carnivores are solitary hunters and foragers but certain otters, mongooses, African Wild Dogs, hyaenas and Lions are social. The mechanisms whereby originally solitary species became social are of the greatest interest.

Limb proportions, body size, gait and colouring all manifest specific adaptations but one of the clearest expressions of adaptive diversity in carnivores is the shape of the head and the relative sizes of ears, eyes and muzzle. Differences in the shape of the head closely relate to the importance of different sense organs and hunting strategies in the different carnivore species. Selective breeding of dogs for different purposes manifests selective breeding by humans, so we can readily appreciate the remarkable transformations wrought by natural selection simply by comparing the shapes of carnivore heads. The Serval, with its big ears, hunts largely by sound, otters rely mainly on vision and whisker-touch, and the jackals, with their long, sensitive nose, depend on scent. The jackal's long tooth-rows snap at prey, while the short, vice-like jaws of the Cheetah serve as clamps. The hyaena's skull is built around bone-cracking teeth and huge chewing muscles (see opposite).

CONSERVATION Apart from direct persecution and destruction of habitats by humans, domestic and feral dogs are a major threat to very many species of wild carnivores. Dogs harass or kill most wildlife within one or more kilometres of their home bases. Sustained over years, this persecution eliminates all but the most agile or arboreal species. As settlement spreads, the baneful influence of dogs (and their diseases) affects an ever-larger part of Africa's natural ecosystems. Domestic and feral cats have similar but more localised effects.

DOGS AND ALLIES CANIFORMIA

An evolutionary grouping of canids, mustelids and pinnipeds (and non-African bears, raccoons and pandas).

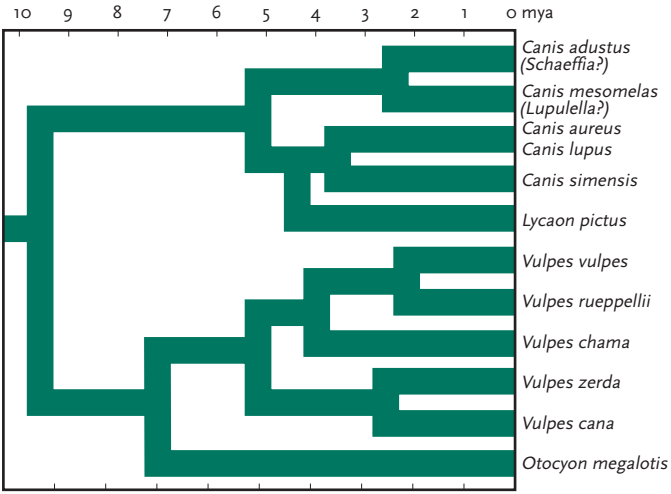
DOGS AND ALLIES CANIDAE

Wild Dog, jackals and wolves	*Canis* (6 species)
Bat-eared Fox	*Otocyon megalotis*
Foxes	*Vulpes* (6 species)

These relatively long-legged, long-muzzled carnivores are adapted to running down prey, or foraging on the trot in relatively open and dry environments. Most have a bushy tail and compact feet with four functional toes.

Separation into fox and wild dog lineages began outside Africa. However, the Bat-eared 'Fox' clearly evolved at an early stage as an African termite-eating specialist (it probably shares ancestry with the Eurasian Raccoon-dog, *Nyctereutes*). True foxes have been unable to maintain a hold in tropical Africa, in spite of having traversed the continent in the past. Nevertheless, one species survives in temperate South Africa.

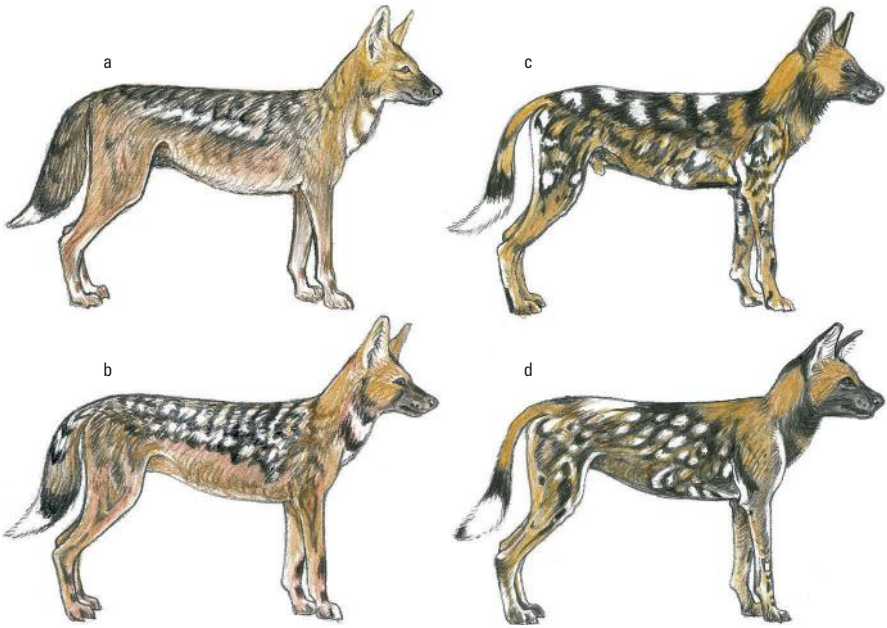
Modern genetics have brought an entirely new perspective on canid evolution in Africa. The African Wild Dog, so distinctive visually and long thought to deserve the genus '*Lycaon*', to itself, has been shown, genetically, to be a true dog, *Canis*. Of all the *Canis* species, it has probably had the longest tenancy in Africa, where its piebald patterns and social behaviour are likely to have evolved quite fast through intense intra-specific selection. Ancestral *Canis adustus* and *Canis mesomelas* were also early in Africa, whereas the Ethiopian Wolf *C. simensis*, the Common Jackal *C. aureus*, and the Grey Wolf *C. lupus* all came in later from Eurasia. Closely related to one another, superficially similar and sometimes hybridising, African wolves and Common Jackals were long judged to be a



Tentative phylogenetic tree for African Canidae (after Lindblad-Toh *et al.* 2005, Wayne & Ostrander 2007).

single highly variable 'Common Jackal'. It has taken more disciplined observation and sophisticated contemporary genetics to confirm the co-existence of two species (as well as wolf/jackal/dog hybrids, to confuse the issue, in parts of the north and west Sahara and in Ethiopia and Eritrea).

Jackal species, each with a preferred habitat, but with substantial overlaps, have different origins. The Side-striped Jackal is the 'oldest' and most versatile species in both diet and behaviour



Pelage pattern formation in African Wild Dog *Canis pictus*. (a) Generalised, semi-cryptic formation in genus *Canis*, as expressed in various jackals and wolves. (b) Similar pattern becoming more conspicuous through enhanced tonal contrast. (c) African Wild Dog pelage in which *Canis*-like format has been dislocated but elements are still perceptible. (d) Wild Dog pelage in which dislocation has generated typical 'marbling' (individual from Longido, N Tanzania).

and has the widest range south of the Sahara. Fossils reveal that the Black-backed Jackal is known to be a very stable species, present in southern and East Africa for several million years. It is exclusive to semi-arid areas of the south–east biogeographic realm and is split into two populations. A much later arrival, the Common Jackal is a Eurasian, desert-adapted form that has colonised the Sahara and arid East Africa.

The difficulties that non-African immigrant fauna sometimes have in sustaining a foothold in Africa can be illustrated by the Ethiopian Wolf. Although well adapted to a specialised diet of highland rodents today, this species almost certainly originated as a consequence of a southward expansion (probably during an ice age) of an early Eurasian proto-wolf or 'coyote' population that originally took more diverse, probably larger, prey. Persistently persecuted by humans, it has long been a naturally rare and localised species (now the rarest canid in Africa – a reproach to the conservation record of past Ethiopian governments).

Canids have evolved special patterns, markings and hair tracts to communicate with one another. In some instances canids can transform their appearance to intimidate other species. Thus the tiny-toothed Bat-eared Fox can chase off much larger animals by fluffing out its crest and tail, all the while snapping fearlessly and ferociously. Like several other canids, its markings neatly outline and emphasise every gesture. African Wild Dogs (*Canis pictus*, their scientific name means, literally, 'painted dogs') exhibit a conspicuous marbled pattern that sometimes resembles that of domestic breeds, such as Australian Cattle Dogs or 'Blues'. 'Painted Dogs' and 'Blues' have derived their patterns, independently, from wolf-like ancestors (see illustration opposite), one by natural selection, the other through artificial selection by humans. Both demonstrate how rapidly selection can alter visual appearances.

Prehistoric human hunters first learnt to manipulate canid behaviour as they slowly, step by step, became mutually inter-dependent hunting teams – human and wolf each selecting each other!

WILD DOG, JACKALS AND WOLVES *Canis*

African Wild Dog	*Canis (Lycaon) pictus*
Side-striped Jackal	*Canis adustus*
Black-backed Jackal	*Canis mesomelas*
Common Jackal	*Canis aureus*
Ethiopian Wolf	*Canis simensis*
Grey Wolf	*Canis lupus*

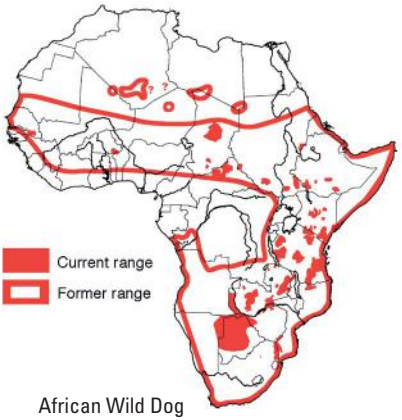
AFRICAN WILD DOG *Canis pictus*

(Note: The former generic name, *Lycaon*, is available as a subgenus of *Canis*.)

OTHER NAMES Painted Dog, Hunting Dog. Fr. *Lycaon*. Ger. *Hyanenhund*. Swah. *Mbwa mwitu*.

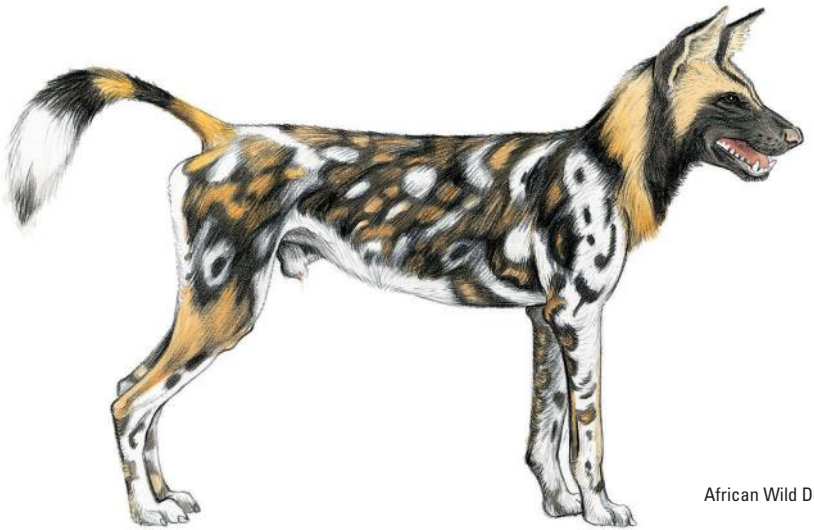
MEASUREMENTS HB 760–1,120cm. T 300–410mm. W 18–36kg.

RECOGNITION A large, blotchy dog with prominent, round ears and a tufted tail. The tail tip is almost always white and the broad, powerful muzzle always black. Each individual's pattern of blotches is unique but there are family and regional resemblances (smaller, darker and more 'marbled' in the east, larger, lighter and more piebald in the south). Although generally silent, a repetitive bell-like hoot, low but penetrating, serves as a contact call while staccato twittering accompanies any reunion or social excitement. The African Wild Dog has a very pungent and distinctive body odour.



African Wild Dog

DISTRIBUTION Formerly throughout non-forested, non-desert areas of Africa. The range is becoming ever more fragmented.



African Wild Dog

HABITAT Woodlands, savannas, grasslands and steppes at all altitudes. African Wild Dogs formerly existed wherever there was sufficient prey susceptible to their 'visual-chase' hunting techniques.
FOOD Exclusively mammals. African Wild Dogs prefer to feed on the commonest medium-sized antelopes not more than twice their own weight (larger animals are also taken, but less regularly). Small animals are eaten entirely but, with larger ones, only the meat and viscera are stripped off and rapidly bolted. As specialised pack-hunters, African Wild Dogs rely on an unconcealed fast chase of up to 5km at a steady 48km/h pace. During short spurts (usually less than 2km) they can exceed 60km/h. Their strategy is to snap and tear at the rear and sides of running prey until it tires.

BEHAVIOUR The social behaviour of a pack centres on a breeding pair, with non-breeding adults assisting in the feeding (by regurgitation) of litters that can number up to 16 puppies. All pack members are subordinate to the breeding pair (which can be distinguished by their tendency to urine-mark). Every pack member is part of a same-sex hierarchy but females are more mobile between packs than the males (males tend to expel or kill intruding males). Packs travel over home-ranges of 200–2,000km^2. Smaller packs always give way to larger ones and the young are known to have a higher survival rate in large packs. Today, an average African Wild Dog pack includes about six adult males and four adult females, but, in the past, aggregations of hundreds of African Wild Dogs were reported.

African Wild Dogs

African Wild Dogs have a slight breeding peak during the late rains. Puppies are born blind and helpless in a burrow (usually one previously dug by an Aardvark or porcupine). They emerge from the burrow after 1 month and are weaned off their mother's milk, onto meat regurgitated by the pack, by 5 weeks. Able to follow the adults by about 9 weeks and adult at about 1 year. Relatively short-lived and few survive to 10 years.

African Wild Dog society appears to be based on the seamless extension of infantile behaviour into adult life. Infantile begging becomes an adult tactic to coerce

others. Immediate effects are to induce regurgitation of meat: social benefits are to initiate 'carer responses' in potential aggressors. Any animal can switch from juvenile to adult role according to circumstances. Often both parties try to outdo each other in the intensity of their begging behaviour, all twittering and mouth-tugging from exaggerated prostrate positions.

Each morning, or after a long rest, awakening youngsters (and adults) will circulate, mobbing others as if trying to force them to regurgitate food in a unique 'meet' ceremony. To avoid being mobbed, each individual seeks out a partner (preferably a gang) with which to form a temporary alliance, and switches role to that of mobber. In rare instances mobbing can turn into serious threats, suggesting that the evolutionary beginnings and original purpose of ganging up against individuals might have been to test fitness. However, in its present form the main purpose of the 'meet' appears to be social coercion and mobilisation of individual animals into a hunting pack.

ADAPTATIONS The tight clustering of African Wild Dogs at the daily 'meet' ceremony, with its emphasis on inclusion and avoidance of isolation, would appear to have a bearing on their unusual colouring. Early explanations interpreted marbling as a form of camouflage, however, strong contrasts hardly conceal the dogs from potential prey. A more likely explanation is that the marbled markings help to create a visual experience of inclusion and merger, during puphood, and then in a circling cluster of dogs during their 'meet' ceremonies.

STATUS Of all African carnivores, African Wild Dogs have suffered the greatest contraction of range in the shortest time. Take-over of land for livestock, direct persecution and diseases from a burgeoning population of domestic dogs are mainly responsible. A short-lived species, Wild Dogs are dependent on frequent and large litters to replenish numbers and on unimpeded access to fluctuating prey populations. To sustain itself this needs a spread of populations and minimum numbers. If Wild Dogs decline too much with populations too far apart, their extinction could be quite swift. Wild Dogs have been exterminated in many countries and IUCN has listed the species as endangered.

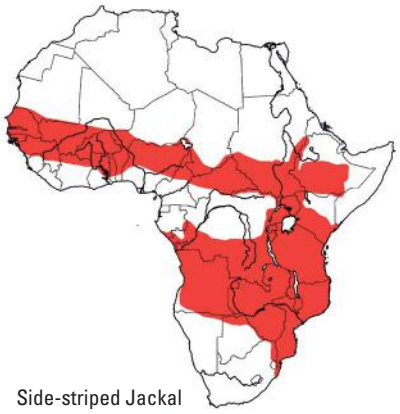
SIDE-STRIPED JACKAL *Canis adustus*

(Note: as a genetically early branch of *Canis*, the subgenus '*Schaeffia*' has been proposed for this species.)

OTHER NAMES Fr. *Chacal à flancs rayés*. Ger. *Streifenschakal*. Swah. *Bweha*.

MEASUREMENTS HB 700–800mm. T 350–450mm. W 7.3–12.0kg.

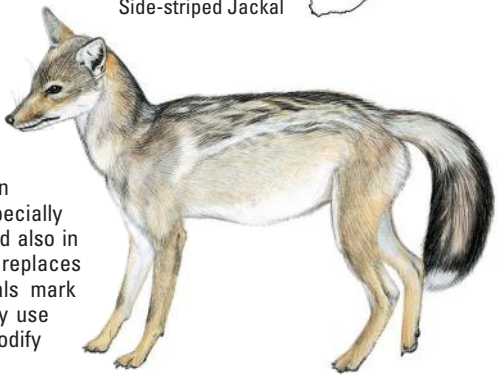
RECOGNITION Drabber, shorter-legged and shorter-eared than other jackals, this species can, in eastern and southern Africa, be distinguished by a white tip to its tail and by poorly defined black-and-white stripes along the flanks, but coat patterns are variable. Mainly nocturnal but also active at dawn and dusk.



Side-striped Jackal

DISTRIBUTION Ranges in a broad band both north and south of the main forest belt (which it has penetrated in the wake of settlement). Absent from the drier parts of southern, north and north-east Africa.

HABITAT Various savanna and thicket types to the edges of forest. Common in various montane habitats up to 2,700m, especially in disturbed vegetation and cultivation, and also in swamps and moist flood-plains (where it replaces the Common Jackal). Side-striped Jackals mark their territories with scats and urine. They use natural dens where possible and often modify termitaries for their own use.

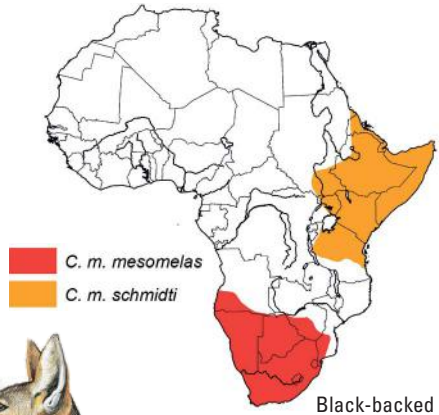


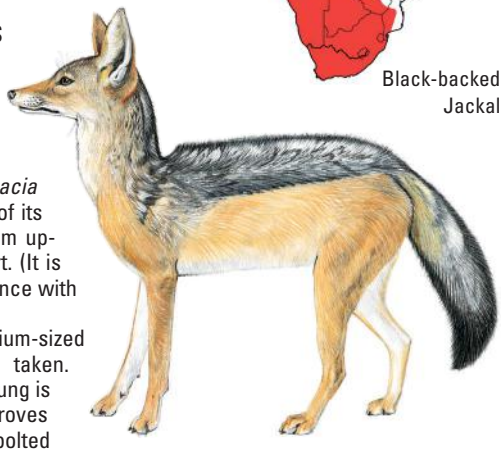
FOOD Omnivorous. Diet very responsive to local resources. Invertebrates and small vertebrates (including fish, stranded or in shallows, and gazelle fawns) are taken, as well as fallen fruits, unripe maize, carrion and organic rubbish.
BEHAVIOUR Pairs defend territories. They may travel as a family group but more frequently move individually. The Swahili name '*Bweha*' derives from the characteristic explosive bark of this species but it has a wide repertoire of growls, yaps, cackles, whines and screams. A croaking distress call elicits intense interest in other members of a family group. 'Howling' is more like hooting in this species.
ADAPTATIONS Shorter proportions, more skulking habits and great flexibility of diet in diverse habitats suggests that these jackals occupy the 'tropical fox' niche and suggests that they may be a factor contributing to the absence of foxes from central Africa.
STATUS Not endangered.

BLACK-BACKED JACKAL

Canis mesomelas

(Note: as a genetically early branch of *Canis*, the subgenus '*Lupulella*' has been proposed for this species.)
OTHER NAMES Fr. *Chacal à chabraque*. Ger. *Schabrackenschakal*. Swah. *Bweha nyekundu*.
MEASUREMENTS HB 700–1,000mm. T 300–350mm. W 6.5–13.5kg.
RECOGNITION Slender, long-legged jackal with large ears and a black back (streaked with white). Limbs and flanks are variously fawn to rufous. The tail is black-tipped.
GEOGRAPHIC VARIATION *C. m. mesomelas* (S Africa), *C. m. schmidti* (NE Africa).
DISTRIBUTION Horn of Africa, East Africa and southern Africa.

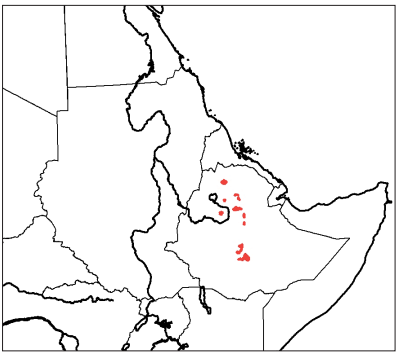




Black-backed Jackal

HABITAT The Black-backed Jackal could be called the Acacia Jackal because of its close association with dry *Acacia* savannas. However, in the southern part of its range it occupies most habitat types, from upland veld and mountains to coastal desert. (It is constrained in the north-east by co-existence with other jackals.)
FOOD Omnivorous but small and medium-sized mammals and carrion are frequently taken. Cooperative hunting by parents rearing young is often assisted by older offspring and improves the survival chances of the pups. Food is bolted and regurgitated in response to the pups' begging.
BEHAVIOUR Black-backed Jackals form more hierarchical family groups than the Common Jackal, in which subadult or young adult 'helpers' are less cooperative in assisting their parents to raise pups. Parents and siblings are very protective of pups and may attack other predators, such as hyaenas, near the den. Vocal communication in southern Africa (where they are the only jackal) includes howling. In areas of overlap, only the Common Jackal howls. Other calls are a loud explosive yelp followed by shorter, shriller yelps. Loud yelps signal alarm. Black-backed Jackals also utter a clattering distress call and a dog-like 'woof' when startled.
ADAPTATIONS Intensive guarding behaviour of the young may reflect high risks from larger predators in areas where both predators and prey are at high densities. Their brighter, more contrasting colour pattern is also consistent with less cryptic behaviour. Black-backed Jackals harass prey and some competitors and are generally more aggressive than other jackal species.
STATUS Treated as vermin in pastoral farmlands. Not endangered.

ETHIOPIAN WOLF *Canis simensis*



Ethiopian Wolf

OTHER NAMES Simien Fox. Fr. *Loup d'Abyssinie*. Ger. *Aethiopienfuchs*.

MEASUREMENTS HB 900–1,000mm. T 250–340mm. W (♀) 11.5kg, (♂) 14.0–18.5kg.

RECOGNITION A tall, large-eared, dog-like animal, rich russet-red above, with white underparts and a black tip to the tail. The long, narrow muzzle ends with a somewhat 'squared-off' nose and upper lip. It has splayed, well-reinforced canine teeth. Highly vocal, its calls include group yip-howls, a yelping bark, a two-phase bleating and an explosive scream.

GEOGRAPHIC VARIATION *C. s. simensis* (north-west of the Rift), *C. s. citernii* (south-east of the Rift).

DISTRIBUTION Once widespread over Ethiopian uplands, but now restricted to relict populations in Simen, Mt Guna, NE Shoa, Bale and Arsi massifs.

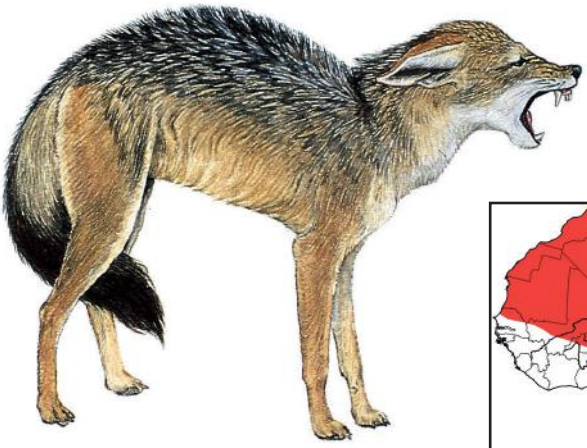
HABITAT Mainly afroalpine meadows and *Helichrysum* moorlands in areas of high rodent density. Packs regularly patrol the boundaries of their territories, marking them with urine and faeces as well as by frequent howling. They scrape shallow hollows or rest on the midden mounds of Giant Root-rats (which generate warmth and provide ambush sites for their favourite prey).

FOOD Giant Root-rats (*Tachyoryctes macrocephalus*) comprise nearly 40% of the prey captures (and the main mass of the diet) on the Bale massif. Smaller rodents (mainly murids), hares and carrion make up the balance. Ethiopian Wolves are solitary foragers but, very occasionally, a pack will hunt antelope or small livestock. Root-rats and rodents are ambushed, stalked, pounced on or excavated. Less frequently they are also snatched in wild scampers across rodent warrens. Foraging is mainly diurnal (as is rodent activity) at higher altitudes but human interference probably explains crepuscular or wholly nocturnal activity in the declining northern populations. (In undisturbed habitats rodent biomass may periodically reach 3,000kg per km^2.)

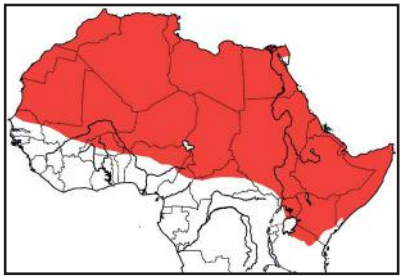
BEHAVIOUR Cohesive, highly hierarchical packs live in regularly demarcated territories of 5–15km^2. A typical pack includes two or more adult females and about five closely related adult males, together with the current offspring of the dominant pair (subordinate females occasionally have pups but tend to desert them in favour of staying with the pack). Pack members forage individually but meet up several times a day to rest, play or sleep together (or to feed pups and the mother by regurgitation). They also meet up to boundary-mark and, while breeding is in progress, they rest up close to the mother's den. The texture and colour of the female's coat changes during breeding, becoming woollier and yellower.

ADAPTATIONS Genetic analyses have suggested that Ethiopian Wolves have an early, Holarctic, coyote-like ancestry. However this is apparently overlaid by elements shared with the Eurasian Wolf (*Canis lupus*). In spite of the restricted range, small habitat and rodent-catching behaviour of the Ethiopian species, its specialisations are modifications of typically flexible and generalised canine behaviour. As Ethiopian ecosystems degraded and cooler habitats retreated higher, the wolves may have shrunk back into an ever-smaller range and refined their skills at exploiting the very numerous rodent prey. With a longer history as tropical species, some jackal species and African Wild Dogs have probably always inhibited the expansion of Ethiopian Wolves out of their cool, Eurasian-like enclave.

STATUS IUCN rates as highly endangered. Unless the Bale Mts plateau is given its promised national park status and agricultural/pastoral conversion is reversed, the Ethiopian Wolf and numerous other animals and plants, many of them endemic, are certain to become extinct. Domestic and feral dogs brought into this formerly uninhabited region by recent settlers have introduced disease, competition and genetic contamination to wolf populations. The habitat is being degraded by an invasion of people and livestock into a very fragile ecosystem and direct killing of wolves is accelerating. At last count some 220– 300 animals were estimated to remain in the Bale/Arsi massif. Northern populations are unlikely to survive under current conditions.



Common Jackal

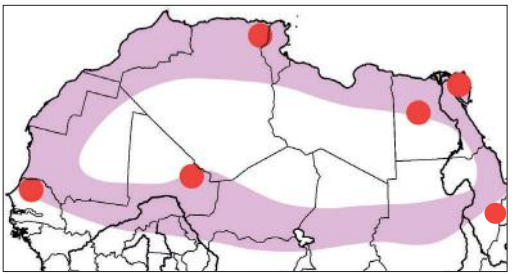


COMMON JACKAL *Canis aureus*

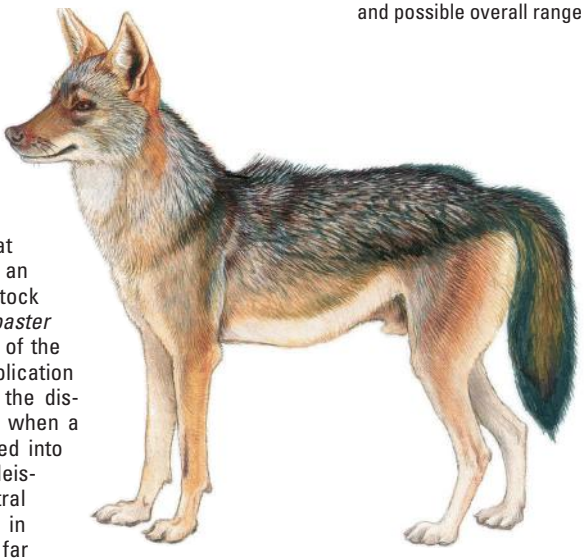
OTHER NAMES Golden Jackal. Fr. *Chacal commun*. Ger. *Goldschakal*. Swah. *Bweha dhahabu*.
MEASUREMENTS HB 650–1050mm. T 180–270mm. W 6–15kg.
RECOGNITION Sand-coloured jackal with a black-tipped tail. The back has streaks of black-and-white hair scattered irregularly through the fawn body colour. Until recently identifications of 'common jackals' embraced what was thought to be an exceptionally variable species. Contemporary genetics has confirmed that slender *Canis aureus* is distinct from robust *Canis lupus lupaster* but that hybrid *aureus/lupus* individuals have served to blur the distinction. *Canis lupus* is profiled separately in this edition.
GEOGRAPHIC VARIATION Twelve races have been named but hybridisation and individual variation has concealed regional differences.
DISTRIBUTION A late arrival in Africa with the parent population scattered right across south and western Asia as far as Burma. In Africa patchily across the Sahara and Horn of Africa south to open plains in N Tanzania.
HABITAT Dry, open country from sea level to over 3,000m. Flourishes around villages and small towns. Depends on secure burrows or dens (self-dug or modified), especially on open plains.
FOOD Omnivorous. Invertebrates and small vertebrates (up to the size of a small gazelle) are taken. Bulbs, berries, fallen fruits and cucurbits are also eaten when available. Feeds at night, in the early morning and evening.
BEHAVIOUR Territorial pairs with their offspring may hunt socially. Several families may form group territories where there is access to super-abundant resources (i.e. rubbish tips). Grown offspring frequently help their parents rear young siblings. Its Arabic name *Ibn awee* is onomatopoeic for the high-pitched howling which allows individuals or groups to locate one another. The barks and yelps resemble those of dogs.
ADAPTATIONS Drought resistance and the ability to subsist without water is the principal determinant of its extensive range.
STATUS Not endangered (but has been exterminated in some localities by poisoning).

GREY WOLF *Canis lupus*

OTHER NAMES African Wolf *Canis lupus lupaster*. Fr. *Loup grisatre*. Ger. *Wolf*.
MEASUREMENTS HB 830–1,100mm. T 310–450mm. W (est.) 8.0–16.5kg.
RECOGNITION Wolves are naturally variable but relatively frequent crossing with dogs and Common Jackals inserts hybrid wolves/jackals/dogs into a situation where confusion between the two species has reigned for more than a century. The taxon *lupaster*, first coined in 1833 to name a North African canid, has, over the years, been applied to describe a distinct species of canid, a subspecies of the Common Jackal and, in 1981, to differentiate North African wolves from jackals. Today the name '*lupaster*' isolates a genetically discrete clade of canid that seems to have first emerged as an African isolate from the same stock as *Canis aureus*. So, could *lupaster* plausibly describe a subspecies of the Common Jackal? The new complication for such a simplistic picture is the discovery by geneticists that later, when a *lupaster*-like population emigrated into Eurasia (maybe in the Plio-pleistocene), it gave rise to ancestral wolves, eventually culminating in the great Timber Wolves of the far north. Much later, a population of Asiatic *Canis aureus* entered Africa. Here it encountered its African cousins, and, in spite of their lengthy separation, they occasionally hybridised, generating fertile offspring. African wolves have a heavier muzzle, broader forehead, thicker neck, a 'hackle' over the shoulders and a grizzled dark-grey mantle above paler, more freckled, ochre flanks. It has required contemporary genetics to justify treating *lupaster* as a wolf rather than an early type of desert jackal. Observing which canids attacked their flocks, Tuareg herdsmen needed no geneticists to name two species.



Grey Wolf: six localities identified for *C. l. lupaster* and possible overall range



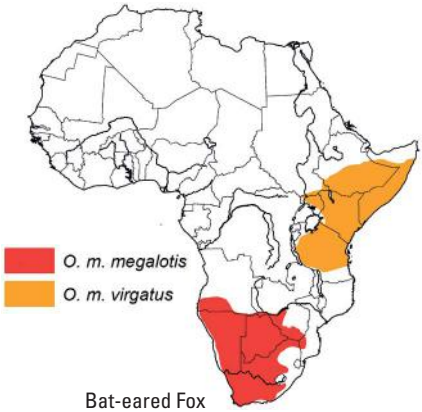
DISTRIBUTION Few fully authenticated localities in Egypt, Ethiopia, Senegal, Mali and Hoggar make any mapping of total range problematic. It is probably realistic to view their range as once nearly pan-Saharan but this was compromised by the later incursion of Common Jackals. The supposed distribution shown here is tentative, provisional and subject to future revision.
HABITAT Wide-ranging and adaptable to many habitats. Formerly likely to have ranged over many habitats now under settlement. Digs dens or uses natural holes or other refuges.
FOOD Omnivorous. Takes many types of vertebrates but propensity to kill livestock, sheep or goats has invited frequent retaliation. Can also survive on invertebrates and small vertebrates; fruits may also be eaten when available.
BEHAVIOUR May hunt socially. Distinctions from jackals and degree of genetic input from dogs await further study.

BAT-EARED FOX *Otocyon megalotis*

OTHER NAMES Fr. *Otocyon*. Ger. *Löffelhund*. Swah. *Bweha masigio*.

MEASUREMENTS HB 470–660mm. T 230–340mm. W 3.0–5.3kg.

RECOGNITION Long-limbed, large-eared 'foxes' with a thickly furred, black-tipped tail and black-tipped ears, feet and muzzle. The eyes are contained within a dark 'mask'. The lightly grizzled upperparts are grey, with an ochraceous undercolour. In some respects their coat pattern resembles that of the Eurasian Raccoon-dog, *Nyctereutes*. Relatively quiet, they occasionally utter a series of thin, wailing howls. Contact calls among Bat-eared Foxes are bird-like mewings.



Bat-eared Fox

GEOGRAPHIC VARIATION *O. m. megalotis* (SW Africa), *O. m. virgatus* (E and NE Africa).

DISTRIBUTION Restricted to arid areas of the Kalahari region and NE Africa, from sea level to dry plateaus and uplands inland.

HABITAT Dry, open country, especially *Acacia* savannas and associated plains and grasslands.

FOOD Termites, especially harvester termites (*Hodotermes*), beetles and other invertebrates; also, marginally, small vertebrates and fruits. Subterranean insects are located by sound, with the ears pitched horizontally to get a fix before rapid excavation. The very dense fur helps protect against the bites of soldier termites.

BEHAVIOUR A permanent pair is the basic social unit, often accompanied by up to six recent offspring. The young are born blind and helpless after a 60-day gestation in a burrow dug (or modified) by the parents.

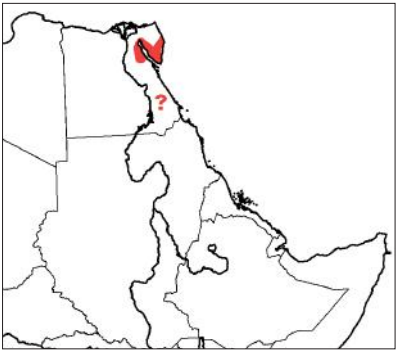
ADAPTATIONS Bat-eared Foxes have between 46 and 50 sharp, cusped teeth, the largest number known for any non-marsupial land mammal. This extraordinary dentition is adapted for slicing-up hard-shelled and pincered insects. Live insects are macerated almost instantaneously because the mandible can chop up and down at least five times a second (because of a special muscle arrangement at the back of the jaw). The enlarged ears, both external and internal, allow Bat-eared Foxes to pick up the sounds of underground prey, while the strongly clawed forepaws allow rapid excavation.

STATUS The magnificent thick fur of this species fetches high prices under its commercial name of 'Macloutsie'. Bat-eared Foxes are extensively trapped for their pelts in Botswana and may be absent or rare in the vicinity of some towns. Not endangered.

Special muscle arrangement at the back of the jaw on Bat-eared Fox.

FOXES *Vulpes*

Royal Fox	*Vulpes cana*
Fennec Fox	*Vulpes zerda*
Cape Fox	*Vulpes chama*
Pale Fox	*Vulpes pallida*
Rüppell's Fox	*Vulpes rueppelli*
Red Fox	*Vulpes vulpes*



Royal Fox

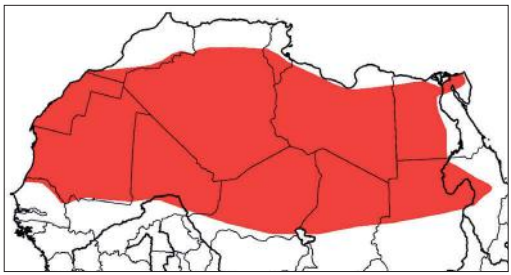
ROYAL FOX *Vulpes cana*

OTHER NAMES Blanford's Fox, Hoary Fox. Fr. *Renard royal*. Ger. *Königlich Fuchs*.
MEASUREMENTS HB 400–600mm. T 290–415mm. W 2–3kg.
RECOGNITION A densely furred, sandy-coloured fox with 'frosted' grey sides, white underparts and a sandy tail that has densely packed, very long, dark guard hairs. Large, funnel-like ears are scantily haired on their inner surfaces and the eyes are set in a narrow brown 'mask' that extends to the corners of the mouth. The general demeanour is very cat-like and animals are invariably evasive and timid but are able to make bounding leaps of astonishing speed and height.
DISTRIBUTION Recently discovered in NE Egypt, this fox ranges from Pakistan to Sinai but is only known from a few localities.
HABITAT Marked preference for rocky mountainous regions up to 2,000m. Possibly the relic of an ice age fauna. Thought to prefer natural crevices and rock shelters.
FOOD Insects, supplemented by fruits and small vertebrates.
BEHAVIOUR Live as monogamous pairs in very small territories. The Royal Fox is extremely sensitive to sound and very shy, escaping notice with a fast ground-hugging run.
ADAPTATIONS The exceptionally dense fur implies adaptation to very cold conditions and Iranian furriers call the pelt Siah Rubah or 'Royal Fox' because of its luxurious texture. The volume of the tail almost matches that of the body (a possible decoy against larger predators). The muzzle is short and delicately tapered but molars are exceptionally deep, sharp and narrow.
STATUS Very rarely seen, this fox might actually range down the entire Red Sea ranges, possibly as far as Ethiopia. IUCN rates as of least concern.

FENNEC FOX *Vulpes zerda*

OTHER NAMES Fr. *Fennec*. Ger. *Fennek*.
MEASUREMENTS HB 370–410mm. T 180–210mm. W 0.8–1.5kg.
RECOGNITION A very small, rather short-legged fox with huge ears and a very small, pointed muzzle. Upperparts are tawny (with a very fine grizzle on the back). The underside, legs, face and ear linings are white. Both the extreme tip of the tail and the fur over the 'violet gland' are black or dark brown. The fur is very fine, soft and dense. The loud call is a brief shuddering howl, descending in pitch and repeated serially. It is strictly nocturnal.
DISTRIBUTION Central Sahara to N Red Sea; also N Arabia.
HABITAT Sand-dune deserts and steppes with light, sandy soils. Self-dug burrows are extensive

Fennec Fox



and dry grass is brought in to line the resting chamber.

FOOD Favours desert grasshoppers and other desert invertebrates. Lizards, rodents and birds, and occasionally fruits and roots, are also taken. The Fennec Fox is an extremely fast and efficient digger in sand, both to catch prey and to escape detection. It can survive without surface water.

BEHAVIOUR The Fennec Fox is most frequently seen in pairs but up to 10 animals have been recorded in a group. Up to five blind and helpless young are born in a burrow after about 50 days' gestation. They are suckled for 2 months and are mature by 6 months. Captive groups are very vocal and sociable, uttering chattering, whimpering and wailing calls as well as growls, chirps and screams. It puts up a spirited defence against dogs or captors. **ADAPTATIONS** The huge external ears are matched by greatly enlarged inner ear bullae and most subterranean food is found by hearing. **STATUS** Common in the central Sahara, the Fennec Fox is in decline wherever settlement and domestic or feral dogs and cats are present. Insufficiently known.

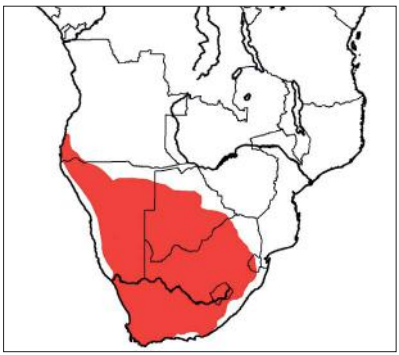
CAPE FOX *Vulpes chama*

OTHER NAMES Silver Fox. Fr. *Renard du Cap*. Ger. *Kapfuchs*.

MEASUREMENTS HB 540–620mm. T 290–395mm. W 2.5–3.5kg.

RECOGNITION A lightly built, slender fox, with bushy tail, medium to large ears and a fine-tapered muzzle. It has a grizzled grey back and russet ear backs and limbs. The face, underside and base of tail are tawny cream. The tip and margins to the tail, and the muzzle stripe, are sepia to black. The loud call is a high-pitched 'wow', ending in two or three yaps. It is a nocturnal animal.

DISTRIBUTION Drier parts of SW Africa from S Angola to the Cape and outer margins of the Kalahari region.

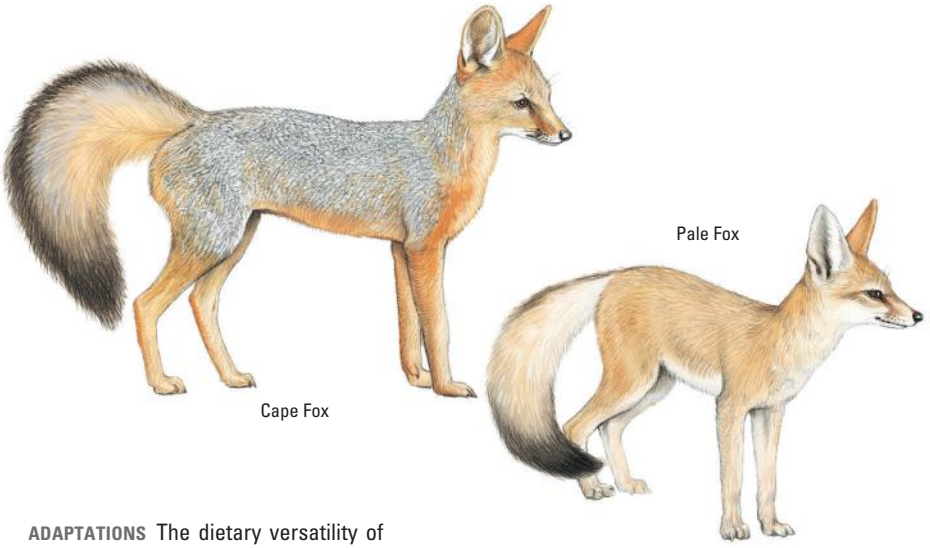


Cape Fox

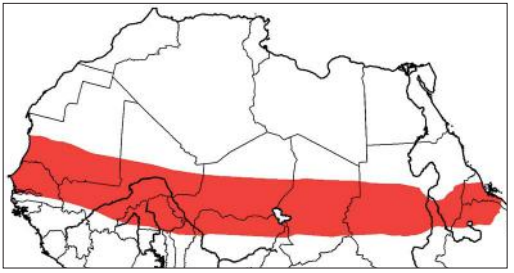
HABITAT Open *Acacia* grasslands, steppe, subdesert scrub and open grassy areas within bushland. The Cape Fox digs burrows or lies up in dense vegetation during the day.

FOOD Predominantly invertebrates and mice; also other small vertebrates, carrion, fallen fruits and grass.

BEHAVIOUR The Cape Fox forages alone but females have been observed out with subadult young. There are one to five young per litter. Males are not seen to associate with females except at mating. Limited records suggest that most births take place during the warm, wet summer period.



ADAPTATIONS The dietary versatility of the Cape Fox and its adaptation to cooler temperate climates would appear to have facilitated its colonisation of SW Africa. However, it is not as abundant as jackals and Bat-eared Foxes.
STATUS Officially persecuted for 100 years, many Cape Foxes were killed without research to justify their supposed vermin status. Not endangered, although locally depleted.



Pale Fox

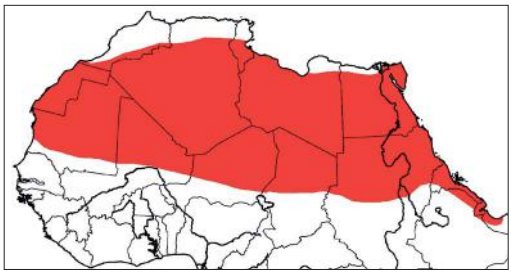
PALE FOX *Vulpes pallida*

OTHER NAMES African Sand Fox. Fr. *Renard pâle*. Ger. *Blassfuchs*.
MEASUREMENTS HB 380–450mm. T 230–280mm. W 2.0–3.6kg.
RECOGNITION A small, very pale fox with large ears, long legs and a relatively thin coat. It has sandy-fawn upperparts and a pale to white underside. There is some variation in the intensity of the colour. The tail is black-tipped and there is black above the weakly scented 'violet gland'.
GEOGRAPHIC VARIATION *V. p. pallida* (Sudan), *V. p. oertzeni* (Chad basin), *V. p. edwardsi* (W Africa).
HABITAT S Sahara and Sahel from Mauritania to the Red Sea, in steppe country, sandy and stony deserts. Pale Foxes dig extensive burrows and tolerate heat well. They are active from dusk till dawn. They are unable to tolerate totally waterless conditions, although they can survive very protracted hot, dry seasons (presumably on the residual moisture in their prey).
FOOD Small vertebrates (mainly rodents and lizards) and invertebrates.
STATUS A little-known African endemic fox with a very extensive distribution within an unstable and fluctuating ecological band lying between true desert and the sub-Saharan savannas. IUCN rates as of least concern.

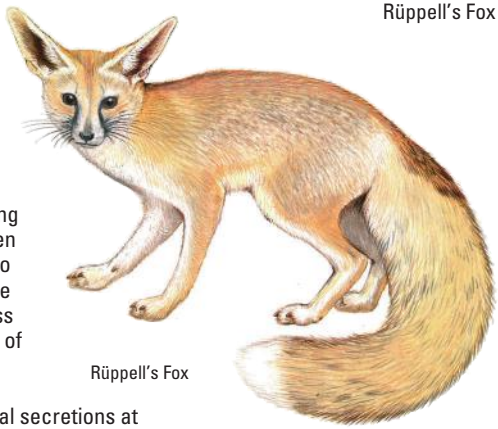
RÜPPELL'S FOX *Vulpes rueppelli*

OTHER NAMES Fr. *Renard du désert*. Ger. *Rüppelfuchs*.
MEASUREMENTS HB 400–480mm. T 250–380mm. W 2.0–4.5kg.
RECOGNITION A very large-eared, slender fox with a soft, thick coat and rich, bushy tail. The grizzled fur tends to be greyish on the sides, with a sandy-yellow or brown flush on the midline (from forehead to tail), elbows and heel. Apart from black whisker patches, the ears and face are very pale, as are the underside and limbs. The tip of the tawny tail is white and above its 'violet gland'

(near the root) is dark brown. The loud call is a harsh, yelping bark. This is a strictly nocturnal, cool-adapted fox.
GEOGRAPHIC VARIATION *V. r. rueppellii* (Egypt and Sudan), *V. r. somaliae* (Eritrea and the Horn), *V. r. cufrana* (Libyan desert and Kufra).
DISTRIBUTION Central Sahara, Libya, Egypt and the Red Sea coast to NW Somalia. Probably of Asiatic origin.
HABITAT Sand and stone deserts where burrows are commonly excavated under slabs of stone or the roots of bushes.
FOOD Rodents, reptiles, insects and occasional fruits (dates). Rüppell's Foxes can tolerate a total absence of water.
BEHAVIOUR Commonly solitary or in pairs, this very vocal species has brittle hacking calls, a high-pitched whistle, trilling (when tense) and hissing (in warning). There is also a barking loud call. Breeding is thought to be seasonal, with three or four blind helpless young born in late winter after a gestation of just under 2 months.
ADAPTATIONS The most striking adaptation is the skunk-like ability to squirt noxious anal secretions at potential predators.
STATUS Common in all non-dune areas of the Sahara. However, this species is known to retreat wherever Red Foxes, feral dogs, and cats have become established in desert settlements. Insufficiently known.



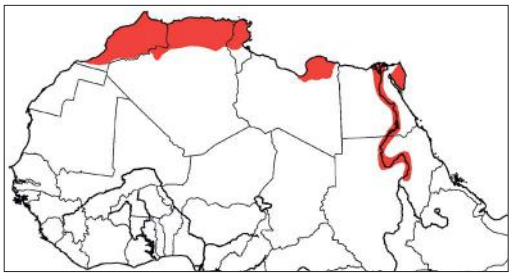
Rüppell's Fox



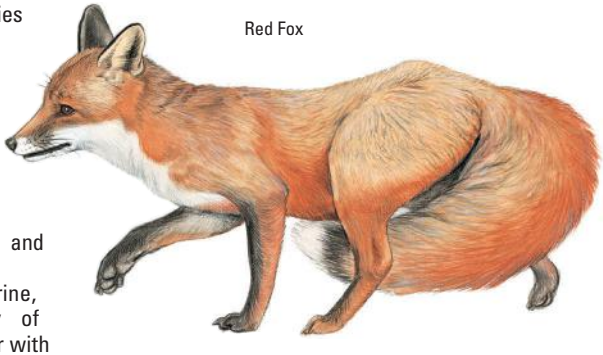
Rüppell's Fox

RED FOX *Vulpes vulpes*

OTHER NAMES Fr. *Renard roux*. Ger. *Rotfuchs*.
MEASUREMENTS HB 500–550mm. T 330–400mm. W 4–8kg.
RECOGNITION Externally indistinguishable from populations living on the northern side of the Mediterranean, N African Red Foxes vary individually and by season (they moult into a short summer coat). The back may be sandy red or greyish, surrounded by red or yellowish flanks, limbs, neck, face and tail. Tail tip, throat and chin are white. Ears, nose, whisker patch, forepaws, and sometimes the belly, are black. The most frequently heard call is a loud, multiple wow-bark.
GEOGRAPHIC VARIATION *V. v. barbarus* (NW African coast), *V. v. atlanticus* (Atlas Mts), *V. v. niloticus* (Egypt, Libya, N Sudan). All probably invalid.
DISTRIBUTION N African Mediterranean and Moroccan littoral and Nile valley.
HABITAT Cultivated and urban land, settlements, desertic steppe, scrub, woodlands and hillsides up to 4,500m. Red Foxes dig or modify burrows. Territories have bolt-holes, scent posts on paths, boundaries and food stores. They vary in size from 30 to 4,000ha.
FOOD Omnivorous: vertebrates and carrion, invertebrates, fruits and household debris.



Red Fox

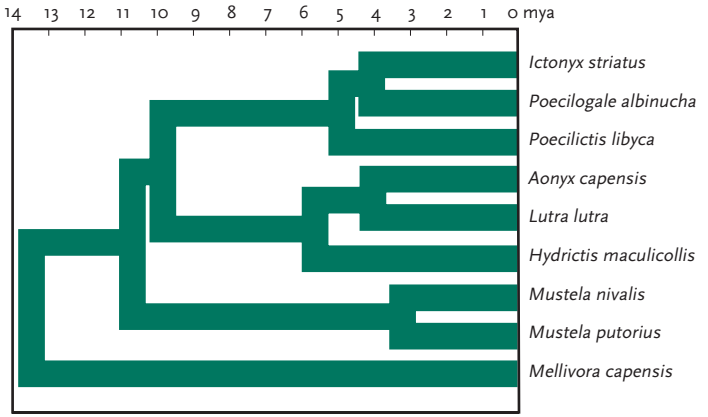

Red Fox

BEHAVIOUR Social grouping varies but pairs occupy large territories in impoverished habitats. Where there is an additional adult female she may be a 'helper'. Tails lashed in greeting dispense scent from the 'violet gland' near the base of the tail. Other scent glands are situated on the lips and between the toes.
ADAPTATIONS Scent marks, urine, faeces and a wide variety of gestures and postures, together with 28 recorded categories of vocalisation, all play a part in Red Foxes' complex social behaviour which helps to explain their status as the most successful small carnivores in west Eurasia. However, they remain subordinate to the Common Jackal in North Africa, and are less numerous.
STATUS Not endangered.

MUSTELIDS MUSTELIDAE

Ratel	*Mellivora capensis*
Weasels and polecats	*Mustela* (2 species)
Libyan Striped Weasel	*Poecilictus libyca*
Zorilla	*Ictonyx striatus*
African Striped Weasel	*Poecilogale albinucha*
Otters	Lutrinae (4 species)

RECOGNITION Medium-sized to small carnivores, generally with a long body and neck, a tubular skull (with a big brain) and shortish legs with five digits. Many species are boldly patterned in black and white, a feature that correlates with anal glands that secrete noxious scents. Short ears imply reduced sensitivity to sound and the eyes too are most sensitive at short range. Scent is the main vehicle for finding prey and communicating with others. All have well-developed canines while tooth-rows have a reduced number of teeth. The jaws and jaw muscles are specialised for killing prey with the canines. All species have very sensitive whiskers and vibrissae.
GENEALOGY Mustelids are of non-African, northern temperate origin and brought their specialisation as fish-, mammal- and bird-predators with them. Some of the earliest African



Tentative phylogenetic tree of African Mustelidae (modified after Sato *et al.* 2012 and Wolsan & Sato 2010).

Mustelid subfamilies: Ictonychinae (African Striped Weasel) (*left*), Lutrinae (African Clawless Otter) (*middle*) and Mellivorinae (Ratel) (*right*).

mustelid fossils, *Eomellivora* (12 mya), *Erokomellivora* (6 mya) and *Howellictis* (7 mya) show similarities with the Ratel. As a very early branch of mustelid, Ratels are likely the oldest mustelid type in Africa. Zorillas are also a distinctively African group, as are the clawless otters. N African mustelids are very recent immigrants from Eurasia. Ratels also occur in Asia but are now commoner in Africa.

ECOLOGY Deriving from cooler habitats, African mustelids are commonest in wet, nocturnal, upland or temperate conditions (see individual profiles).

NATURAL HISTORY Mustelids are predominantly solitary, with sexes living in separate but overlapping territories. Most species use few vocal and visual signals but have elaborated scent as a means to help regulate reproduction and demarcate territories. All female mustelids depend upon stimulation from a protracted copulation in order to induce ovulation. Sustained mating, lasting an hour or more, is assisted by a rigid bone, or baculum, in the penis of the male.

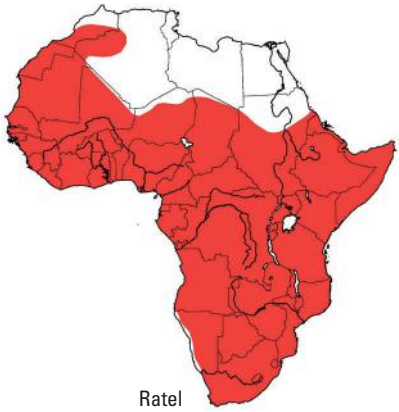
ADAPTATIONS Many mustelids are well adapted to a micro-habitat that includes holes, hollows and tunnels in which they pursue their prey and also find shelter. They are highly exploratory and show good coordination and dexterity. Otters are particularly dexterous. Non-amphibious African mustelids are diverse. Heavyweight diggers or 'badgers' have evolved independently in Eurasia, America and Africa and the more distinctive of these are regarded as subfamilies of their own. Subfamilies in Africa are: Ratels (Mellivorinae), weasels (Mustelinae) and striped weasels and zorilla (Ictonychinae).

RATEL *Mellivora capensis*

OTHER NAMES Honey Badger. Fr. *Ratel*. Ger. *Honigdachs*. Swah. *Nyegere*.

MEASUREMENTS HB 580–780mm. T 160–230mm. W 5.2–14.5kg.

RECOGNITION A chunky, lumbering carnivore with a white forehead and variably coloured dorsal mantle. In some individuals the entire upperside is white or near-white; in others the white forms a narrow boundary between the dark-grey back and black underparts. Other permutations extend to an occasional all-black animal. The neck and shoulders are very muscular and the broad forepaws are armed with massive claws. By contrast, the hindlegs are lightly built, with small claws. The skin is very thick and loose, with coarse, hog-like bristles above and sparse, finer fur below. The ears resemble oblique crevices on the sides of a big, blunt-muzzled head. For its size, the Ratel has one of the largest brains of any carnivore and this is contained within a very hard and heavily constructed skull. If disturbed, a dominant individual bristles, stretches its limbs, raises head and tail while luttering a very loud rattling roar that finds onomatopoeic expression in a number of its local names (e.g. *Entahurra* in Luganda and *Nkarungurungi* in Kimasai).Submissive individuals crouch, lower their head and tail, champ their jaws and squeal. At least 11 subspecies have been named but these are mainly based on variations in melanism of the mantle. Colour morphs appear to lack regional consistency.



Ratel

DISTRIBUTION The whole of Africa except for the driest centre of the Sahara and the Mediterranean littoral. Absent from the Nile valley and Orange Free State, the latter probably due to human agency. Distribution is patchy everywhere and densities are thought to fluctuate considerably.

HABITAT The Ratel is commonest in open woodland but occurs in forest, in waterless desert steppe (with stunted acacias), on high mountains in afroalpine moorland and in coastal scrub.

FOOD Opportunistic omnivore, specialising in the excavation of social insects, mice, trapdoor spiders, dung beetles, larvae, scorpions, etc. from hard, subterranean hiding places. The Ratel also excavates the softer parts of well-protected animals, such as tortoises and turtles. Whenever possible it will take reptiles, birds and even fish. It also occasionally takes larger animals if they are young or otherwise vulnerable. It finds most of its food by broad-spectrum, opportunistic foraging over a wide area (its sustained bouncy gait can cover up to 37–40km in a night). When feeding on bees, termites and army ants, the Ratel usually releases anal secretions which, among other functions, may serve to fumigate/incapacitate the insects, thus facilitating the robbery of their nests. The Ratel readily scavenges carrion and will even appropriate the kills of other carnivores (including, on occasion, those of Lions). In spite of its power, it can be very dainty and precise when feeding on larvae, insects or viscera, picking out individual items one by one. It also caches surplus food, including honeycombs.

BEHAVIOUR Ratels have very large, overlapping ranges, and normally forage singly but two animals are sometimes seen together. Larger groups may be aggregations at common resources (for example 12 animals have been seen digging at a cattle 'boma' where concentrations of dung beetles and their larvae are very high). Males have quite exceptionally large testes in proportion to their size, implying a superproduction of sperm. The social implications of this endowment are uncertain but single males expend much energy roaming areas up to 698km^2 in search of oestrous females. Up to four young are born after a gestation of 50–72 days (captives giving birth 153–162 days after copulation suggest some form of foetal slowing or delay might be possible). Females give birth in a lined burrow, which is usually self-dug but which may be excavated, typically from a termitary. Offspring accompany their mother for up to 6–8 months before becoming independent. The Ratel may live for more than 30 years in captivity.

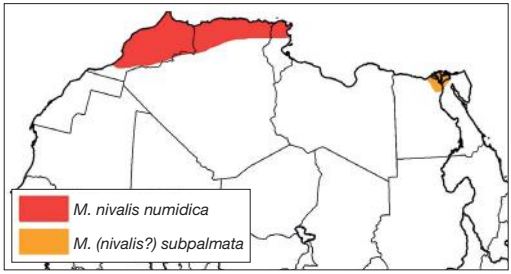
ADAPTATIONS Social insects have a number of effective defences against most predators, but the Ratel is well equipped to breach these. With its spade-like foreclaws, it is able to tear open insect nests while its thick skin and stink glands help to protect it from stings and bites (nonetheless swarms are known to have killed Ratels). It would seem that honeybees inside their hive may be immobilised by chemicals in Ratel anal secretion. Able to locate terrestrial insects by smell. Diurnally active individuals have also been known to exploit typical honeyguide behaviour by following the birds making their regular circuit of visits to bees' nests.

STATUS Areas in which the Ratel has become rare or totally absent are increasing. The reasons for this may include susceptibility to cat and dog diseases. Also as modern apiculture displaces the more fatalistic and tolerant practices of traditional beekeepers, the Ratel is beginning to suffer serious persecution, for example in Western Cape province commercial beekeepers kill Ratels (during 15 years at least 280 animals). It is readily trapped and poisoned in retaliation for occasional raids on hives or on small livestock.

WEASELS AND POLECATS *Mustela*

Common Weasel	*Mustela nivalis* (+ *subpalmata*)
Polecat	*Mustela putorius*

COMMON WEASEL
Mustela nivalis



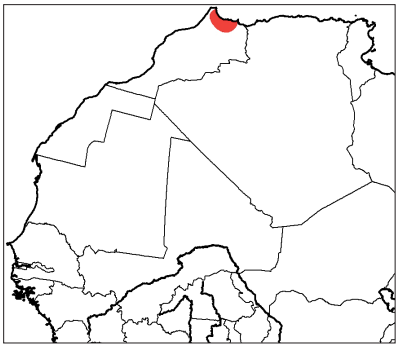
Common Weasel

OTHER NAMES Fr. *Belette*. Ger. *Mauswiesel*.
MEASUREMENTS HB 230–300mm. T 90–130mm. W 190–425g.
RECOGNITION A very small, elongated carnivore with brown or russet upperparts and a white underside. The skull is long and tubular, with mouth, nose and eyes surprisingly small and closely placed. It leaves very small but strongly scented faeces as territorial markers. It utters a sharp alarm call.
GEOGRAPHIC VARIATION *M. nivalis numidica* (Morocco, Algeria and Tunisia), *M. (nivalis?) subpalmata* (Egypt). Whether these two North African forms are species or subspecies remains uncertain.
HABITAT Mediterranean littoral and Atlas Mts, mainly in farmland. In Egypt they also live in urban gardens and wastelands (even entering buildings).
FOOD Rats, mice and cockroaches, in semi-urban environments; frogs, lizards, small birds, rabbits and insects in more rural areas. Prey is hunted by smell in concealed drains, verges, hedges and crevices.
STATUS Common.

M. n. numidica

M. (nivalis?) subpalmata

POLECAT *Mustela putorius*


Polecat

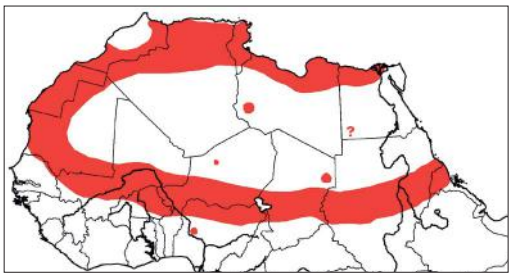
OTHER NAMES Fr. *Putois*. Ger. *Iltis*.
MEASUREMENTS HB 350–450mm. T 120–160mm. W 700–1,500g.
RECOGNITION A long-bodied, furry carnivore with white ears, and face marked with a black eye-mask and hood. On the body, black guard hairs lie over a dense, woolly coat of ochre or sandy yellow. Legs and tail are black or deep brown. If disturbed or attacked, the Polecat chatters or screams and discharges a strong, disagreeable odour.
GEOGRAPHIC VARIATION *M. p. furo*. Strabo (58 BC to AD 24) wrote that domestic Ferrets originated in N Africa. It is therefore possible that Moroccan

Polecats are either ancestral to Ferrets or that they are Ferrets that have been feral for 2,000 years or more.
HABITAT From sea level up to 2,000m in the Atlas Mts west of the Riff. Polecats are found under dense cover in woodlands, secondary scrub and in farmland, and often around barns and outhouses near villages.
FOOD Small mammals, reptiles, frogs, birds and insects; very occasionally fish and fruits.
STATUS Inadequately known.

Polecat

LIBYAN STRIPED WEASEL *Poecilictis libyca*

OTHER NAMES Fr. *Zorille de Lybie*. Ger. *Streifenwiesel*.
MEASUREMENTS HB 230–300mm. T 160–190mm. W 200–250/350g.
RECOGNITION A conspicuous, small carnivore with long, erectile hair, mainly white upperparts and narrow black stripes down the back. Underparts, eye-mask and forehead band are black. The tail is white. Black-and-white markings vary individually and regionally. This weasel wanders openly at night, usually with the tail carried vertically above the back. If approached it growls, fluffs its fur and presents its anus. A spray of choking, nauseous anal secretion deters a closer approach.
GEOGRAPHIC VARIATION *P. l. lybica* (southern (Sahelian) range), *P. l. vaillantii* (Mediterranean range) (but a polymorphic species).
HABITAT Sahara desert, mainly on its margins and mountains. A nocturnal species, it lives in dry stony country and sandy subdeserts. Although it has been observed in wooded country, it prefers more open steppes with sparse bush. It digs burrows at the base of dunes and can hide in rock crevices or in the burrows of other animals.
FOOD Rodents and other small mammals, reptiles, invertebrates, birds and their eggs. Prey is mostly dug out of the ground after being trailed by scent. In spite of its deliberate, often slow, movements the Libyan Striped Weasel can pounce and kill prey very rapidly.
STATUS Widespread. Little known.

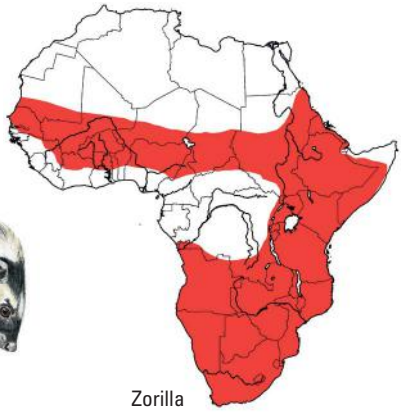


Libyan Striped Weasel

ZORILLA *Ictonyx striatus*

OTHER NAMES Fr. *Zorille commun*. Ger. *Zorilla*. Swah. *Kicheche*.
MEASUREMENTS HB 280–380mm. T 160–300mm. W 428–1,460g.
RECOGNITION A small carnivore with strong claws on the forelegs, black underparts and a well-furred white tail. Back boldly striped in black and white, face piebald in various permutations. Short ears have white margins. Zorillas squirt noxious anal secretions at any attacking predator: may also sham death by lying limp (always with the pattern of black dorsal 'diamond' with two white stripes facing the aggressor).
GEOGRAPHIC VARIATION Twenty-two subspecies have been described with three regional groupings as follows: *I. s. striatus* (S Africa), *I. s. erythrae* (NE and E Africa), *I. s. senegalensis* (W Africa).

Zorilla

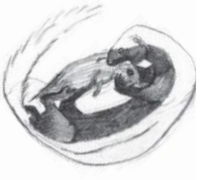

Zorilla

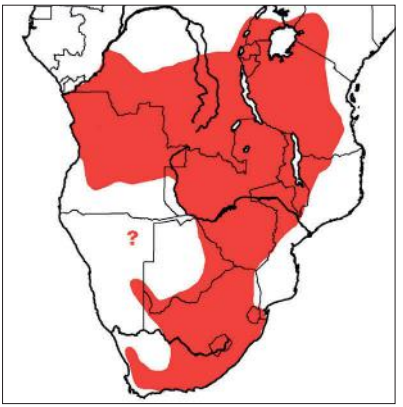
DISTRIBUTION Sub-Saharan Africa, except forest and moist woodland zone; also rare or absent in part of Somalia.
HABITAT Very patchily distributed, being scarce or absent in most heavily wooded areas. Commonest in cool, well-grazed upland grasslands and steppes. Where well established, uses habitual paths and appears to know its home-range well.
FOOD Opportunistic, invertebrates main staple but rodents form bulk of diet in some localities during certain seasons. Snakes and other reptiles also commonly taken in some localities. Hares recorded. Food is found during the cooler part of the night, most hunting between 22.00 and dawn. Moves with a springy, fast trot but can stalk and pounce on prey in spite of its striking coloration. Much prey, notably mice, dung beetles, larvae and lizards, is found by smell and dug out of shallow burrows. Dangerous snakes or large rats are wounded by sudden deep bites and may be shaken or wrenched. Bites are repeated until prey no longer able to bite back.
BEHAVIOUR Several Zorilla families have been kept together in captivity, where mutual grooming appears common. Normally encountered as solitary foragers; peaceful cohabitation in captivity suggests that they may not have exclusive territories. However, exclusive core areas are likely as adult males are mutually intolerant and females avoid them except while in oestrus. Pups are born blind, naked and immobile after a 36-day gestation. Eyes only become functional by about 40 days but development thereafter rapid. Young Zorillas accompany their mothers for several months after leaving the breeding den at about 2 months. Females are fertile by 9 months and can be about with their first litter of two to four young before they are 1 year old.
ADAPTATIONS Zorilla anal secretions are nauseating and also highly irritating to the eyes. The squirting of noxious anal secretions is common to many other mustelids, as well as some mongooses and a few species of fox. It evidently evolved to deter predators and it also appears to play a role in the regulation of social life. In situations of conflict subordinate Zorillas scrape their forequarters on the ground while keeping their backsides raised and ready to squirt.
STATUS Late-night activity means that Zorillas are rarely seen and they remain little known. Very widespread, although localised. Not endangered.

AFRICAN STRIPED WEASEL *Poecilogale albinucha*

OTHER NAMES White-naped Weasel. Fr. *Poecilogale à nuque blanche*. Ger. *Weissnachenwiesel*. Swah. *Chororo*.
MEASUREMENTS HB 250–360mm. T 130–240mm. W 230–350g.
RECOGNITION A small, very elongated carnivore with very short legs but powerfully clawed paws and a conspicuous black-and-white striped back. The crown and tail are white and the underside black. In spite of regular grooming, local earth colours may stain the animal's fur so that it appears red, yellow or grey (especially during the rains). The gape is very wide and the canines are proportionately as long and sharp as those of a Leopard. The gait is distinctive. While walking slowly with the nose to the ground the body is arched or extended. Periodic halts are marked

African Striped Weasel





African Striped Weasel

by rising from the haunches to sniff or peer around. Often it will swing the forequarters from side to side as if to get a visual 'fix'. Both halt movements give a remarkably snake-like impression.

GEOGRAPHIC VARIATION Six subspecies have been named but these are probably not valid.

DISTRIBUTION SE Africa from E DR Congo and Uganda to the Indian Ocean as far south as Cape Province; also westwards through central Africa to Angola. Known up to at least 2,200m altitude.

HABITAT The African Striped Weasel occurs in numerous widely separate localities, which suggests that the present climate of Africa may be less favourable to it than in the past. Main centres of distribution are uplands with extensive grasslands or high veld with perennial, dense rodent populations. At higher altitudes may be about at dawn or dusk but otherwise is strictly nocturnal. Digs burrows but is often associated with termitaries.

FOOD Almost exclusively rodents, with occasional birds and eggs. The African Striped Weasel is a specialised rodent-catcher and can eat three or four in a night. The mouse or rat is simultaneously seized in the jaws and paws while the weasel rolls over and over, yanking the prey with vigorous kicks. This dislocates the neck and renders the prey immobile. In this state it may be eaten, carried or stored in the home burrow.

BEHAVIOUR Normally seen singly or, less often, in pairs. Larger groups (up to four) include pairs as well as single females with young. Home-ranges marked with smeared faeces and urine at regularly used sites. Weasels purr in greeting but scream loudly when fighting. Copulations only occur under shelter and can last for well over an hour! Females give birth to up to four very undeveloped young (weighing only 4g) after a 1-month gestation. They remain blind for more than 7 weeks and are only fully mobile at 11 weeks, at which time they are weaned and begin to follow the mother (a weasel family travelling in file greatly resembles a disarticulated snake). Young pups are carried by the nape, which has a white mane and very thick skin.

ADAPTATIONS The elongated body and small proportions of the African Striped Weasel allows it to dig out rodents but also follow them down their burrows. Its technique of immobilising prey allows for the temporary storage of live mice, which may be critical for a predator with a super-active metabolism.

STATUS Isolated populations might be vulnerable to land clearance and habitat change. In general, not endangered.

OTTERS Lutrinae

Spotted-necked Otter	*Hydrictis maculicollis*
Common Otter	*Lutra lutra*
Congo Clawless (Swamp) Otter	*Aonyx congicus*
African Clawless Otter	*Aonyx capensis*

Otters are long-bodied, long-tailed, amphibious carnivores with dense waterproof fur, a blunt, short face and a prominent moustache of whiskers. The hindlegs (the main means of propulsion in the

water) are more or less webbed. The hands may also be webbed or have dexterous, clawless fingers. Within a species there can be very considerable differences in size, and clawless otters, in particular, can grow to impressive proportions. (An extinct otter, *Enhydrion*, is estimated to have weighed 250kg, well over twice the weight of an adult human!)

Eurasia is their most likely continent of origin but the two *Aonyx* species probably diverged within Africa. *Lutra* and *Hydrictis* are more recent arrivals.

All otters are patchily distributed: absent in areas without permanent water, appropriate food or adequate feeding conditions. In the past, high densities of crocodiles may have been a local deterrent.

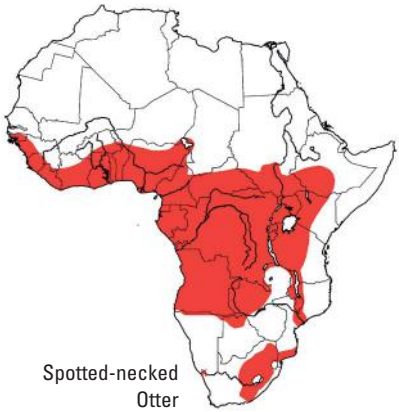
Otters have a high metabolic rate and require regular, frequent feeding on high-energy foods. Clawless otters are tactile fishers, find food in muddy, turbid waters and have flexible diets and hunting ecologies. Fish otters (*Lutra* and *Hydrictis*) are visual, active hunters. Typically follow cycles of more or less tolerance toward their own species, normally dispersed as solitary foragers or small family groups but form larger groups where resources permit. All species make loud attention calls as well as penetrating whistles. All use natural riverside retreats or 'holts' to raise their young. African Clawless Otters and Congo Clawless (Swamp) Otters are externally so similar that they are difficult to tell apart. Their teeth, however, are so different that dental taxonomists have treated them as separate genera or subgenera. The huge, plate-like molars of the African Clawless Otter are clearly adapted to crushing the shells of crabs, molluscs, turtles and catfish heads, but their shallow rooting in the skull suggests that this was a relatively late development.

All otters are hunted for their fur; they are susceptible to trapping, hunting with dogs and drowning in fishnets. Fish-farming is the primary cause of conflict in many areas. Nylon-net fishing is depleting otter populations by drowning them in many inland waters.

SPOTTED-NECKED OTTER

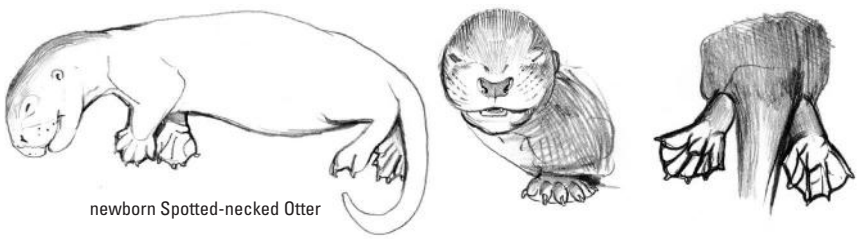
Hydrictis maculicollis

OTHER NAMES Fr. *Loutre à cou tacheté*. Ger. *Fleckenhalsotter*. Swah. *Fisi maji mdogo*.
MEASUREMENTS HB 600–650mm. T 350–400mm. W 4.0–6.5kg.
RECOGNITION A sleek, slender otter with a long tail and well-webbed, clawed toes. Apart from the brown-and-white blotching of the throat and underparts, which is very variable, the colour is a uniform, deep chocolate brown. Older individuals or regional populations may show paler, more ochre or grey tints. It leaves dung deposits on prominences and midstream rocks. A thin, high whistle is the most characteristic call.
GEOGRAPHIC VARIATION Seven races have been described (one from a 20km² lake). All are probably invalid.



Spotted-necked Otter

DISTRIBUTION Scattered thinly over the wetter parts of sub-Saharan Africa but may be locally common in the Great Lakes and in some wet montane regions. Absent from the far west, SW, and NE and East Africa.



newborn Spotted-necked Otter

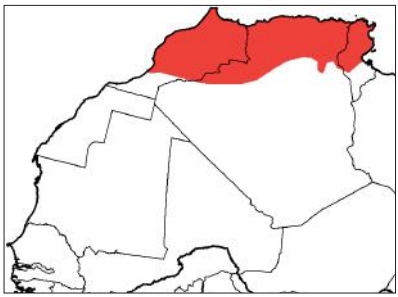
HABITAT Clear water seems to be an important determinant in the Spotted-necked Otter's distribution (it is mainly a diurnal fisher). In many lakes and rivers it shows a preference for rocky, undisturbed areas without turbid inflow. It is present in mountain streams (where fish appear not to be abundant) but absent from many fish-rich but turbid rivers in East Africa. It is also absent from all shallow alkaline lakes of the Eastern Rift. It is a poor colonist (or recolonist) perhaps because it requires permanent and continuous waterways for dispersal.
FOOD Fish and frogs; also crabs, molluscs, aquatic insects and larvae, and various other vertebrates and invertebrates. Conspicuous, slow-moving fish up to 60cm long (preferred size 10–20cm) and frogs are favoured. In undisturbed areas the most intensive feeding periods are the 2 or 3 hours after dawn and before dusk, but midday and moonlight hunting have also been observed.
BEHAVIOUR Usually solitary, but may form small family parties. It forms groups of up to 20 animals in L. Victoria. Some of these groups include both sexes while others are apparently aggregations of young males. Females give birth to up to three blind, helpless cubs in a sheltered burrow or crevice after a gestation period of 2 months. Offspring stay with their mother for nearly a year. Can be very vocal and utters an aggressive trilling, a long, mewing contact call, shrill chattering and various spluttering snorts.
ADAPTATIONS This species relies on clear water and visual hunting. Although dextrous, this is a 'mouth-oriented' otter rather than a 'finger otter', like members of the *Aonyx* group.
STATUS Soil erosion near the sources of major rivers may be a more insidious threat than nylon nets and direct destruction by fur-trappers or fish-farmers. This otter is still locally abundant but is in retreat in many areas.

COMMON OTTER *Lutra lutra*

OTHER NAMES Fr. *Loutre d'Europe*. Ger. *Fischotter*.
MEASUREMENTS HB 600–900mm. T 350–470mm. W 6–18kg (rarely up to 27kg).
RECOGNITION A brown, amphibious mammal with strong, well-clawed, webbed toes. The short face has prominent eyes and a brush of stiff whiskers on the muzzle. The coat can vary from light tan or grey tints to deep dark brown. The Common Otter makes chirping contact calls and a soft whistle of alarm. It is now forced to be largely nocturnal. Dung left on prominent waterside sites (with oily scent smears nearby) betray its presence.
GEOGRAPHIC VARIATION *L. l. lutra* is the only race in Africa.
DISTRIBUTION Formerly from Morocco to Tunisia.
HABITAT Formerly on inland rivers and lakes as well as along the Mediterranean coastline; now found only in a very few localities. Common Otters need dense vegetation for cover and safe retreats in holes, hollow trees, hulks and culvert drains for breeding.
FOOD Mainly fish but also frogs, crabs and many small vertebrates and invertebrates associated with fresh- or saltwater. They are known to travel 3–10km in a single night's foraging.

Common Otter

BEHAVIOUR Solitary individuals, pairs or families range over 12–24km of shoreline (and some up to 60km) on which they use up to 40 habitual resting spots (each well spaced from the next). Females bear up to five young after a 2-month gestation. The mother depends on a secure, undisturbed shelter and adequate food to raise her young.
ADAPTATIONS Common Otters are mainly visual hunters of active fish which they catch in open pursuit. They require consistent and frequent sources of food.
STATUS Almost extinct in Africa. This species has suffered the effects of water pollution, tree clearance, diversion and drying out of rivers and direct persecution. Endangered.

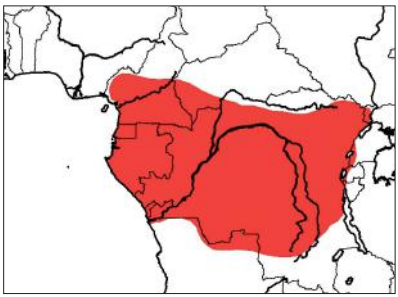


Common Otter

CONGO CLAWLESS OTTER

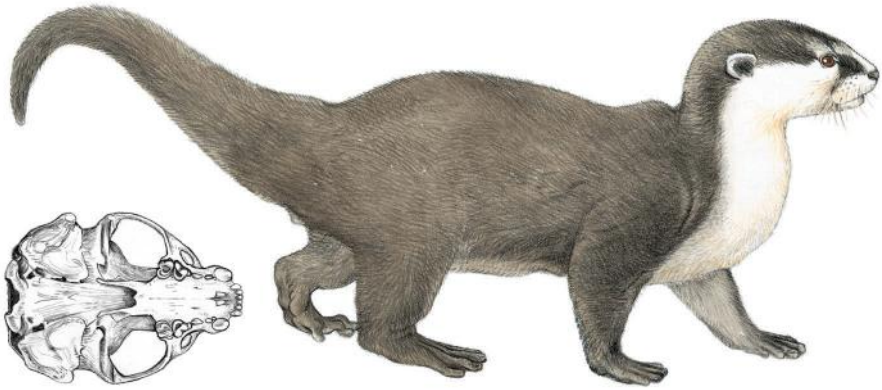
Aonyx congicus

OTHER NAMES Swamp Otter. Fr. *Loutre du Congo*. Ger. *Kleinzahn Fingerotter*.
MEASUREMENTS HB 690–970mm. T 400–590mm. W 15–25kg.
RECOGNITION A very large otter with a white bib, nose and ears and a prominent black patch between the eyes and nostrils. The body colour is rich sepia with some frosting on head and neck. The back of the head and neck are appreciably more slender than in the African Clawless Otter. The molar teeth are smaller and deeply cusped.



Congo Clawless Otter

GEOGRAPHIC VARIATION *A. c. congicus* (Congo basin to Gabon), *A. c. microdon* (rivers off Cameroon highlands), *A. c. philippsi* (mountains of E DR Congo and Uganda to Burundi), *A. c. poensis* (Bioko I.).
DISTRIBUTION Main forest block from E Nigeria to Uganda.
HABITAT Rivers, swamps and ponds close to or surrounded by rainforest. Sightings in (now drained) papyrus swamps in the highland valleys of W Uganda have been reported in the past. In undisturbed areas these otters are active during the day as well as at night.
FOOD Fish, frogs, earthworms, crabs, molluscs and other vertebrates and invertebrates caught in the water, on muddy shores and in backwaters of permanent river courses and swamps.
BEHAVIOUR Excellent swimmers, deft and thorough explorers of the shores of forest rivers and swamps. Animals forage singly but family parties have been observed in Cameroon rivers.

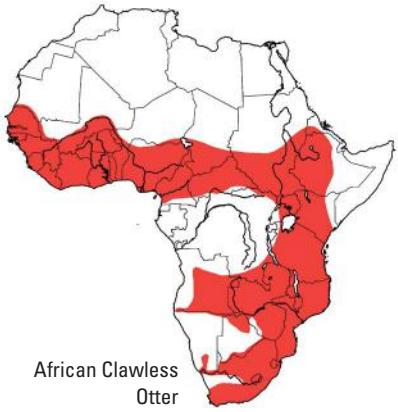


ADAPTATIONS The animals' powerful build provides them with the physical strength necessary for foraging in tangled and muddy riversides. It may also allow them to escape the attentions of most predators as crocodiles, pythons, eagles and Leopards are less likely to tackle large otters. The development of sensitive, clawless fingers is a tropical adaptation best suited to feeling about in mud and cloudy water.
STATUS These otters are much hunted for their beautiful coats. They are common in only very limited localities, rare elsewhere. Vulnerable.

AFRICAN CLAWLESS OTTER

Aonyx capensis

OTHER NAMES Fr. *Loutre à joues blanches*. Ger. *Fingerotter*. Swah. *Fisi maji kubwa*.
MEASUREMENTS HB 1.13–1.38m. T 400–710mm. W 10–18kg (note: 34kg reported was a captive male, but comparable scales have been estimated in the wild).
RECOGNITION A large, occasionally very large, otter, with blunt, unwebbed fingers and toes, and almost vestigial fingernails. Head broad, neck massive, visibly modelled by large neck and jaw muscles. Thick fur and loose skin of body and upper limbs contrasts with tight, short fur on hands and feet. Upperparts vary from very dark chocolate brown to greyish brown or pale tan. Underparts similar except for white or off-white chest, chin and cheeks. Dark area between eye and nostril never sharply isolated (as it is in Congo Clawless Otters). Mantle may be frosted in some individuals. Most frequent signs are single or multiple dung deposits full of crushed crab shells or catfish bones. Waterside resting places, slides or 'holts' (as well as scented retreats in crevices, root and reed tangles or self-dug burrows) are other signs. Utters a loud, attention-catching 'aah'.



African Clawless Otter

GEOGRAPHIC VARIATION Of 11 described subspecies, *A. c. capensis* (S and W Africa), *A. c. hindei* (E Africa, E DR Congo and N Zambia) and *A. c. meneleki* (Ethiopia) are in use.
DISTRIBUTION Very patchy over sub-Sahara from sea level to 3,000m; absent from the central Congo basin. Dependent on permanent water (even if only residual dry-season pools).
HABITAT Rivers, streams, marshes, lakes and dams with adequate cover or concealment; also estuaries and inshore sea close to mangroves or tall cliffs (in SE Africa). These otters forage in swamps and the intertidal zone along southern temperate coasts. Absent from several large rivers and many lakes where a combination of factors exclude them, including parasites, predators such as crocodiles and, particularly, waters that are too fast or otherwise unsuited to their prey or hunting

techniques. They are dependent on shelter, especially when breeding. They can laboriously excavate burrows in soft, sandy and wet soils but usually scrape a form in some naturally sheltered place.

FOOD Freshwater crabs consistently form the major part of the diet. Seasonal changes in crab activity are offset by the ability to excavate aestivating crabs from their dry-season retreats in soft, sandy soil. Crabs are extremely abundant in both permanent and many seasonal river courses. Frogs comprise a lesser, more seasonal, part of the diet, as do fish, small mammals, birds and molluscs. The latter may be smashed at chosen rocks (leaving small shell middens) but mussels are usually a fall-back resource. Food is found by thorough exploration of both above- and underwater surfaces, most often by touch in turbid water.

BEHAVIOUR Animals normally forage singly or as a mother with young. However, adults may be quite tolerant and spend time together. Possibly related animals along a stretch of 3–20km of river or coast may share a group or clan territory. Have a vocabulary of whistles and squeals (contact), a chirping bark (greeting) and moans, mews and sniffles (young coercing adults). Up to three young are born after about 2 months' gestation. Mothers are very fierce in defence of their young and can inflict deep, damaging bites on dogs or people.

ADAPTATIONS This species shares all primary adaptations with the more generalised Congo Clawless Otter. Specialisation in eating crabs and other hard-shelled foods are secondary adaptations that have enabled these otters to widen their range in a rather dry continent.

STATUS Widely hunted for their fur and in retaliation for raiding fish-farms; dogs are an increasing hazard. Becoming extinct or scarcer in many localities, but still widely distributed.

SEALS PINNIPEDIA

A group of carnivores that have adapted to marine habitats. Their family name means 'fin-feet'. Their bodies have become modified to be extremely flexible, animated torpedoes, able to twist and turn in pursuit of the equally agile fish on which they feed.

Sea lions and fur seals (Otariidae) are less extreme in the modification of their limbs. 'Earless' or 'true seals' form the family Phocidae.

All pinnipeds are thought to derive from ancestors shared with bears and to have evolved in the northern Holarctic. They probably emerged more than 30 mya, most likely in the northern Pacific.

FUR SEALS OTARIIDAE

The Cape (South African) Fur Seal is the only member of this family known from African coasts. Unlike 'earless seals', fur seals have small, but visible external ear pinnae. Fore- and hind flippers are largely hairless, females have four teats. Dives are generally shallower than in true seals.

FUR SEALS *Arctocephalus*

Arctocephalus means 'bear-headed'. The Cape Fur Seal is one of eight rather similar species.

CAPE FUR SEAL *Arctocephalus pusillus*

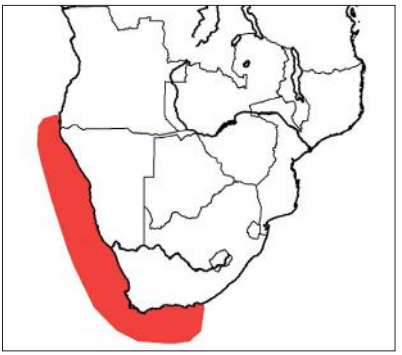
OTHER NAMES South African Fur Seal. Fr. *Phoque du Cap.* Ger. *Kapseehund.*

MEASUREMENTS HB 1.5–2.3m (♂), HB 1.1–1.8m (♀). W 60–350kg (♂), W 22–80kg (♀).

RECOGNITION A large streamlined marine mammal. In spite of its name (*pusillus* = very small; based on an immature pup!) this is the largest of all eight species of fur seals and the necks of adult males, already hugely powerful and muscular, are further enlarged by dense, thick hair. Forelimbs act as highly mobile flippers in the water but bend at the wrist to support the body on land. Hind limbs also retain some ability to support body weight on land, where a clumsy but fast 'caterpillar-gallop' can propel them back into the sea surprisingly fast.

DISTRIBUTION They range down the coastal seas between S Angola and SE South Africa, mainly attracted by the abundant fish of the offshore Benguela Current, but also depend on SW African islands to give birth and rear young. Intense persecution by people and predators in the past might explain the former rarity of colonies on the mainland, but now all the largest colonies are

continental. Diamond mining has prohibited public access to the breeding beaches, where as many as 70,000 young may be born in a single colony each season.



Cape Fur Seal

FOOD Some 34 fish species, 18 cephalopod species, and a few crustaceans have been recorded. The choice of species show strong seasonal differences. Prey is hunted mainly by sight, with attacks made mostly from below. Lactating females are more tied to the vicinity of their pups and juveniles also depend on near-shore fish. Trawlers attract fur seals for 'trash-fish' and offal.

BEHAVIOUR An annual peak in births and copulations leads to congregations of large, very noisy, honking males, which establish small beach territories, mainly in October–November. They posture and confront one another with chest buffets and slashing bites, very occasionally with fatal results. Females tend to arrive later (most in Nov–Dec) just before giving birth. Although highly gregarious, new mothers are fiercely defensive of their immediate space and pup. About a week after giving birth females tend to come into oestrus and are mated immediately, mostly by territorial males. At about this time females must go to sea for food, leaving their young in highly localised creches where new pups clump for warmth and security, bleating like lambs at every disturbance. On return, after 2–4 days at sea, mothers recognise their offspring by scent and by voice but depend on very precise relocation of their birthing spot. Females will search diligently, bawling continuously but will not suckle strange pups – consequently lost pups die. While births are approximately a year apart, research has shown that true gestation is only eight months, after delayed implantation of four months. They can live for more than 30 years.

ADAPTATIONS Cape Fur Seals can dive to depths of 400–500m and can tolerate extremes of cold and heat. However, many very young pups succumb to heat stress. Streamlining and powerful body/limb actions generate great speed and agility in this major marine predator.

STATUS In South Africa the 1973 Sea Birds and Seals Protection Act seeks to protect seals, but some licensed killing of adults and pups is permitted. Shooting of fur seals at sea (ostensibly in defence of trawled fish harvests) is common. However, investigators have concluded that interference and damage by seals is minor compared with the actual value of fish caught by increasingly large-scale modern techniques.

TRUE SEALS PHOCIDAE

Phocidae ('true seals') embraces 19 species and 13 genera. They lack external ear pinnae, have short muzzles, short fur, furry flippers, and entire toothrows have become modified to puncture slippery fish (so cannot be identified as premolars or molars). The earliest fossils have been dated to 29–25 mya.

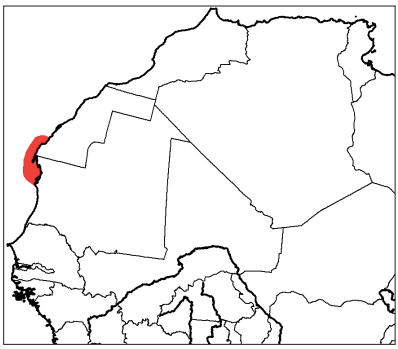
Propulsion in the water is primarily from the rear, but unlike fur seals they cannot rotate their hind limbs under the body and are very clumsy, maggot-like movers on land. They are able to dive deeply, have high concentrations of haemoglobin in their red blood cells and can withstand the strong pressures of the deep sea by exhaling before they dive.

MONK SEALS *Monachus*

The genus *Monachus* is thought to represent an early type of seal. This is particularly evident in the structure of the inner ear.

MEDITERRANEAN MONK SEAL

Monachus monachus



Mediterranean Monk Seal

OTHER NAMES Fr. *Phoque Moine de la Méditerranée*. Ger. *Mittelmeer-Mönschrobbe*.
MEASUREMENTS HB 2,100–2,700mm. T 150–190mm. W 300–335kg.
RECOGNITION An exceptionally elongated, tubular seal. Sexes differ in colour with males darker (near black) than the grey females. Both sexes look piebald during the moult of their exceptionally short-haired pelage. They have large eyes staring out of a broad, flat face, with a prominent moustache of ochre whiskers. Newborn animals are black and woolly.
DISTRIBUTION Formerly all Mediterranean and most NW African Atlantic shores, the Azores, Canary and Cape Verde Islands. Now occurs from the Cabo Blanco peninsula (Morocco-Mauritania), along the Atlantic coast and offshore islands. Formerly most abundant on sand banks and open beaches on mainlands and islands, now mostly restricted to marine caves below steep cliffs. In the Cabo Blanco peninsula (in the absence of human disturbance) breeding females have reoccupied open beaches.

FOOD Coastal or pelagic fishes, crustaceans and cephalopods. Dives normally less than 50m and the maximum recorded dive was around 8 minutes. Larger prey may be taken up to the surface and chewed before swallowing.
BEHAVIOUR Unlike fur seals most behaviour takes place in the water, including copulation but very little is known. In localities where these seals breed in marine caves (probably sub-optimal for that purpose) adult males defend territories outside the entrance to such caves. Breeding does not appear to be seasonal. When females are about to give birth they seek isolated spots above the high-tide line and defend that site from other seals. Offspring can continue being suckled for up to four months. Females known to foster young that are not their own. Once they can swim, youngsters are highly mobile and independent.
ADAPTATIONS This species is primarily an inshore feeder, making shallow dives, and has a physiology and anatomy less adapted for deep diving. As the most primitive of all living seals any shortcomings in its adaptation to diving are of exceptional interest.
STATUS Once abundant over a vast extent of coastline, this seal's fate exemplifies the mindless rapacity of human appetites. Today, the largest known population survives under the cliffs of Costa de las Focas in the Cabo Blanco peninsula where 317 seals were estimated to occur about 1995. This population was reduced by disease to an estimated 103 individuals by 1998. A sub-population in Madeira was last estimated at around 27 animals. Effectively extinct along the Morocco–Algeria coast. Deliberately and incidentally killed to prevent damage to fishing nets and traps. Attrition also due to dynamite explosions, drift-nets, high concentrations of organochlorine compounds (PCBs, DDTs) and heavy metals (mercury, lead, etc.).

CATS AND ALLIES FELIFORMIA

An evolutionary grouping of the Tree Civet, cats, viverrids, hyaenids and mongooses.

TREE CIVET NANDINIIDAE

Modern molecular genetics has demonstrated that *Nandinia* is the sole survivor of a lineage deriving directly from the common ancestral stock from which cats, viverrids, hyaenas and mongooses originated. It has partly cartilaginous auditory bullae (a diagnostic and essentially primitive feature). It also has complex, slightly horny patterns on the plantar surfaces of both front and rear paws.

Tree Civets, the single representative of the genus, are arboreal, nocturnal carnivores with cat-like claws, long, muscular tails and dense, curly fur that half conceals the ears. They have very well-developed perineal and other skin glands. Captives display levels of intelligence seemingly superior to most cats or dogs. They live in predominantly equatorial and montane forests, with scattered, patchy distribution in the east. As highly arboreal omnivores that live an exposed life, mainly in dense forest, Tree Civets depend upon scent to regulate their social contacts and upon a very cryptic coat to escape detection during the day. They are muscular and acrobatic, with exceptional flexibility in all their joints and can sustain the strains of hanging or cantilevered postures, retaining a firm grip with the hindlimbs while manipulating difficult foods with the forelimbs.

Although some Asian Palm Civets (*Paradoxerus*) resemble the exclusively African Tree Civet, even occupying similar niches, they are not closely related, as was formerly thought. The Tree Civet's alternative name of 'Palm Civet' is therefore misleading and has been abandoned in favour of the more appropriate 'Tree Civet'.

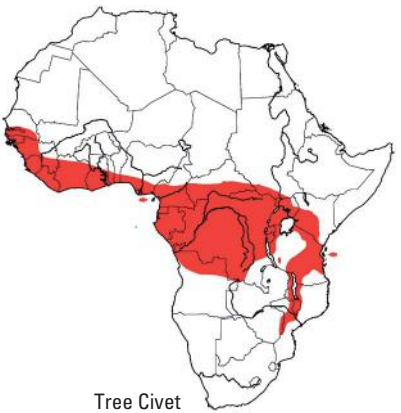
Plantar surfaces of hindfoot (*left*) and forefoot (*right*).

TREE CIVET *Nandinia binotata*

OTHER NAMES Two-spotted Palm Civet. Fr. *Nandinie*. Ger. *Pardelroller*.

MEASUREMENTS HB 450–580mm. T 500–620mm. W 2.0–3.2kg.

RECOGNITION A very inconspicuous, mottled brown, arboreal carnivore with long body and tail, well-clawed feet and distinctively textured soles to the hindlegs. The inner toes on all feet are somewhat separated from the other digits and function rather like thumbs during manipulation of foods or tangled twigs. The strong, flexible limbs allow it to descend vertical tree trunks head-down. It also drops spread-eagled from considerable heights. Two pale spots on the shoulders become prominent during the hunched appeasement gesture. The olive-green eyes have a conspicuously vertical pupil.



Tree Civet

GEOGRAPHIC VARIATION *N. b. binotata* (main forest block), *N. b. arborea* (E Africa to Rufiji R.), *N. b. gerrardi* (SE Africa S of Rufiji R.), *N. b. intensa* (S of Congo R., N Angola).

DISTRIBUTION Tropical forested Africa and moist, montane areas as far south as Zimbabwe. They range from sea level up to 2,000m.

HABITAT Mainly rainforest but also flourish in the cultivation mosaic that follows partial, or even extensive, clearance of the forest. This may be due to their partiality for the fruits of colonising trees, such as the Umbrella Tree (*Musanga*), Sugar Plums (*Uapaca*), Corkwood (*Myrianthus*) and wild figs.

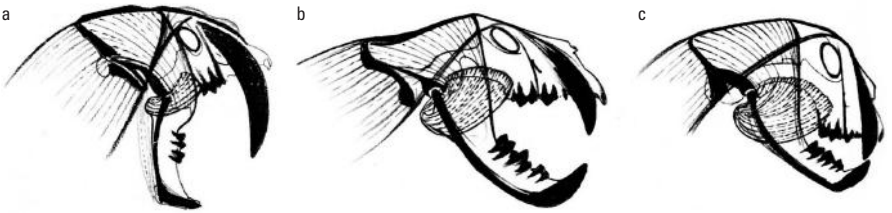
Tree Civet

FOOD The above-mentioned fruits, the fleshy pulp of oil palms and numerous other fruits (including cultivated varieties) form seasonal staples. However, they are omnivorous and highly opportunistic, catching roosting birds, nestlings, rodents, lizards, fruit bats and insects. They also take carrion. Prey is stalked and pounced on, bitten repeatedly and bolted whole or in very large pieces. Animals become active shortly after nightfall, forage for about 4 hours, rest up and then forage again for 3–4 hours before dawn. They hide in a crevice or hole, where available, but more usually in a vine tangle, or even curled up in an exposed tree fork.
BEHAVIOUR Mainly solitary but home-ranges overlap extensively, with a dozen or more animals using a common resource, such as a grove of fruiting trees. Up to four young are born in a hollow tree after a 2-month gestation. There may be two breeding peaks in the late rains. Young accompany their mother while foraging until they are near adult size.
ADAPTATIONS Cryptic colouring limits modes of communication to scent and sound. Contact calls between family members are piping mews and a louder clucking call; they also purr. Aggression is signified by growls, spitting and a burst of screaming, and alarm by a gruff bark. However, scent represents the most important mode of signalling. The primary source of scent is a large sac on the lower abdomen which secretes a copious brown musk. Other scents are produced from the palms of the feet, the chin area and from the belly of lactating females (the latter has a brilliant yellow colour that stains the offspring). These secretions are augmented by anal and urinary scents similar to those of genets. The exact role of this battery of scents in regulating social contacts awaits further study.
STATUS A widespread and locally abundant species that is common on bushmeat stalls in West Africa. Rare in some isolated E African forests. Not endangered.

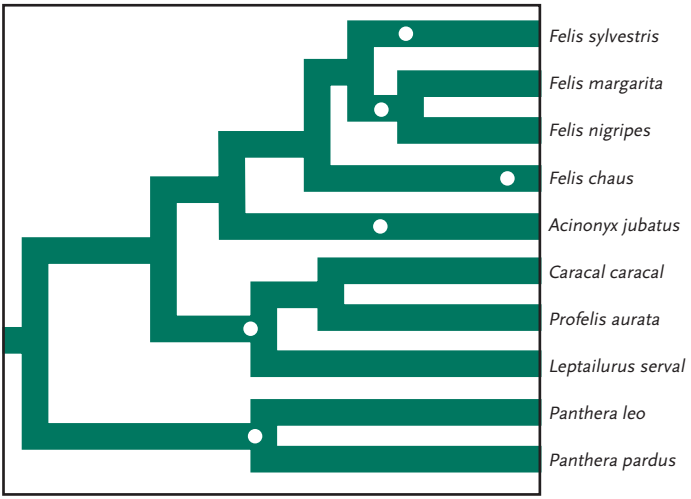
CATS FELIDAE

Lion	*Panthera leo*
Leopard	*Panthera pardus*
Serval	*Leptailurus serval*
African Golden Cat	*Profelis aurata*
Caracal	*Caracal caracal*
Cheetah	*Acinonyx jubatus*
Swamp Cat	*Felis chaus*
Wildcat	*Felis sylvestris*
Black-footed Cat	*Felis nigripes*
Sand Cat	*Felis margarita*

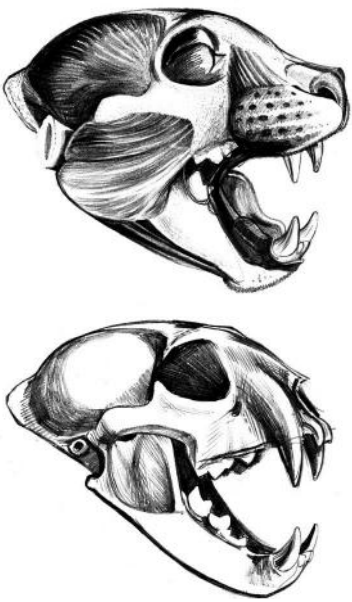
In spite of the modest body sizes of most wild cats, all derive from much larger sabre-tooth ancestors. Progressively declining size is a major characteristic of the modern cat radiation, ranging from Lions, at over 270kg, to little Sand Cats (not much more than 1kg). All cats are built on a very similar body plan: a long body, short, rounded head with large canines served by well-developed cheek muscles. Molars are reduced in number. They have good bifocal vision, acute hearing and an expressive face. All have curved claws (retractile claws being an ancient development in feliforms, though suppressed in some lineages) and relatively soft fur with some degree of blotching or banding. Found all over the world, cats are almost exclusively meat-eaters, at the top of their respective food chains, and each species is highly dependent on an abundance



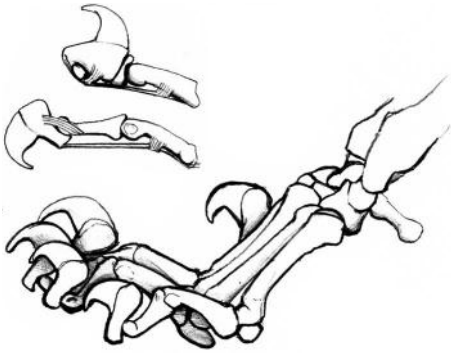
Skull architecture in: (a) *Megantereon cultridens* (stabbing strike); (b) Lion *Panthera leo* (canine bite); (c) Cheetah *Acinonyx jubatus* (clamp stranglehold).



Tentative phylogenetic tree for African Felidae; at least six separate ancestral immigrations into Africa shown (O) (adapted from Johnson *et al.* 2006).



Skull and cranial musculature of Leopard.



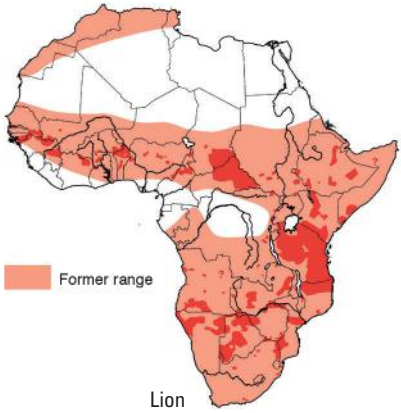
Mechanism for extension and retraction of felid claws.

of appropriate types and sizes of prey. Their presence or absence is therefore an indicator of the relative ecological health or debility of an area.

Cats mark their home-ranges with scent and scratch marks and all species are highly observant, their vigilance being directed at their own species as well as prey and enemies. Because social interactions are potentially dangerous, all species have elaborate appeasement behaviour, including body postures, rubs, lickings, purrs, miaows and tail signals. Scent is a primary mode of regulating contact, augmented by contact calls and scouting from regularly used observation posts. Of all carnivores they are the most efficient killers, clawing into their prey and directing fast, accurate bites to whichever part of the body will lead to a rapid death. All species are in decline.

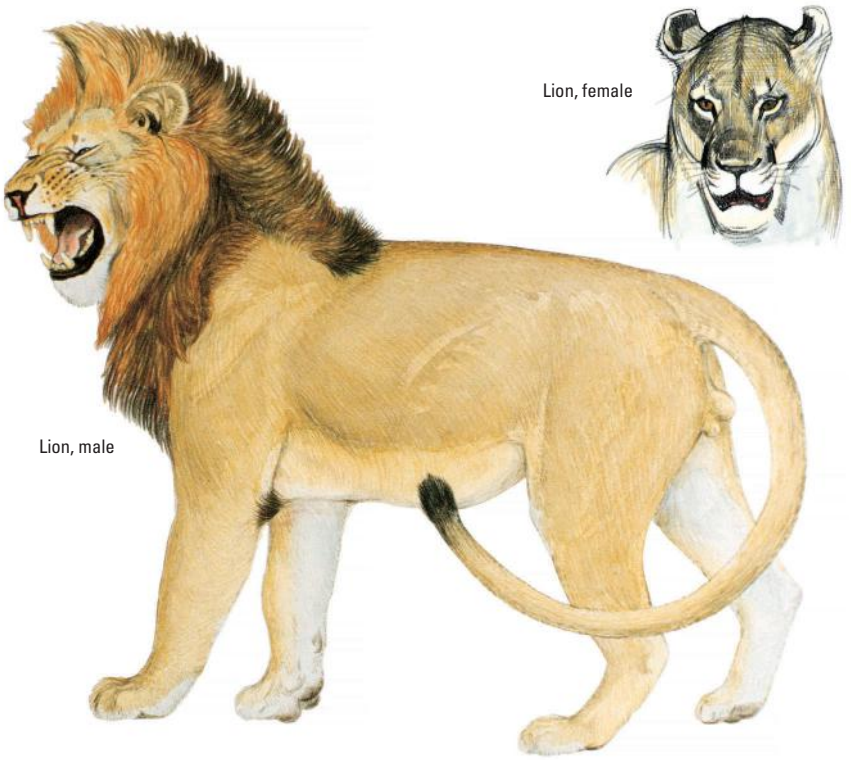
LION *Panthera leo*

OTHER NAMES Fr. *Lion*. Ger. *Löwe*. Swah. *Simba*.
MEASUREMENTS HB 1.58–1.92m (♀), 1.72–2.50m (♂). T 600–1,000mm. SH 1.00–1.28m. W 122–182kg (♀), 150–260kg (♂).
RECOGNITION The largest of the cats, ranging in colour from nearly white to deep ochre-brown. The commonest colour is a tawny yellow but ash grey is not uncommon as a body colour, especially in males. The face has subtle tints and markings around eyes, mouth and ears that enhance facial expressions. Males develop thick, woolly manes that vary individually in colour, length and extent. In populations living in Africa today, manes seldom extend far over the shoulders nor hang in a fringe along the full length of the belly (as they did in extinct forms in N Africa and in the Cape). A bold pattern of Leopard-like rosettes is characteristic of the young but this usually fades and disappears as the animals mature. Both sexes roar (the males more loudly). Roaring starts with a few moans followed by about a dozen full roars that then die away into grunts. On a still night roars will carry for 8km. Roars advertise presence and position, probably also status and identity. Group roaring has the immediate function of reinforcing a pride's identity and solidarity, it also discourages intrusion by nomads and other prides.



Lion

GEOGRAPHIC VARIATION The extinct Barbary and Cape Lions were once treated as subspecies (*P. l. leo* and *P. l. melanochaita*). All Lions are currently considered monotypic.



DISTRIBUTION Formerly most of Africa; now patchily in reserves and national parks but decline continues. Lions once extended through the Middle East to Arabia, Persia and India.

HABITAT Formerly at most altitudes and in all vegetation types, except the most extensive forests and driest deserts.

FOOD Most prey are mammals weighing between 50 and 300kg. When prey of this size cannot be readily caught, any animal between 15 and 1,000kg may be attacked. The smaller are eaten by individual Lions, the heavier killed and eaten by groups. Prey species and their sexes, numbers and condition vary according to season and locality, but the commonest mammals (usually fewer than 10 species) make up most of their diet. During famines, or when the Lion is disabled, rats, reptiles, fish or even groundnuts may be taken. Most prey is caught after a skilled stalk (taking advantage of any type of cover, including dust, vehicles or clouds over the moon) and a fast run or charge. Larger animals are strangled; smaller ones are bitten deeply in the head, neck or chest. In some localities a high proportion of prey is pulled down by females, but males are also very competent killers.

BEHAVIOUR Lion social groups, commonly called prides, typically contain about five (2–20) adult females, two (1–8) adult males and their young and subadult offspring. Individuals spend much time on their own or with one or more companions but a kill, bouts of roaring or more subtle signals periodically reunite dispersed animals. Reunions are marked by much rubbing, leaning, purring, licking and other signs of appeasement by subordinate members and brief fights among seniors. Female-to-female bonds within a pride are persistent and involve vigorous allied defence of the pride's territory against intruding females (occasionally reinforced by help from the males). Males form similar associations but their membership of a pride is more transitory and seldom lasts more than 3–4 years. Frequent challenges from nomadic groups ensures that male Lions enjoy a brief prime (while they are aged 5–10 years) and a short life thereafter. Females are longer-lived, more numerous and provide the continuity in a pride (which is therefore commonly described as matriarchal), but there is a similar, although slower, turnover of female pride members. Both male

and female membership of resident groups of pride Lions is periodically augmented by immigrants drawn from highly mobile, unstable nomadic groups. Nomads wander very widely and provide the means of recolonising empty territories; they also account for most killers of livestock.

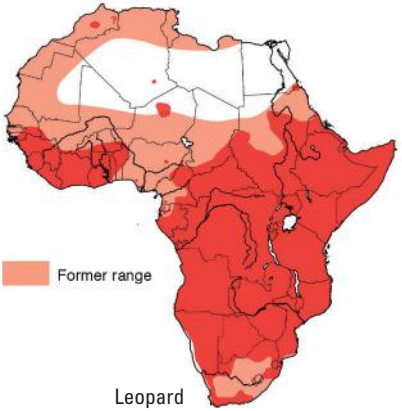
It is common for the females in a pride to come into oestrus simultaneously, resulting in a large number of similarly aged cubs. Although females will suckle one another's cubs, stragglers or weaklings are often left to their own devices and mortality among cubs is very high. Deaths include killings by newly arrived males. Gestation is around 100 days, with two to six young born in a thicket, long grass or among rocks. The rate at which cubs develop and grow varies greatly and 'runts' are frequent. Eyes open between 3 and 11 days, the cubs become mobile at about 1 month, they begin to accompany adults by 2 months, are weaned by 8 months and are independent by 18 months. The young make a sharp 'yip' contact call while mothers grunt at their young. A low, hooting 'woof' (often uttered by a female with cubs and directed straight down at the ground) signifies alarm and can send cubs scurrying into cover. Lions are fully mature by 5 years old.

Lion expressions change through small alterations around mouth, eyes and ears.

ADAPTATIONS Because females reject strangers with great ferocity, the mane, as an imposing 'enlargement' of the Lion's head and shoulders, probably serves to both intimidate and attract females and may assist relatively mobile males to impose themselves on groups of more stable resident females. A Lion in his prime, at about 6 years, has a luxuriant mane that comes into prominence during the 'strut', an artificial tip-toeing gait directed at both females and subordinate males. Intimidation is most effective when two or more males gang up against others. Male associations can be almost as close and lasting as those between females. However, it is only possible for many males to join up with many females in areas where a rich year-round crop of meat can sustain them all. Such conditions, once very widespread, were a likely precondition for the evolution of all-female prides and of big-maned male gangs.

STATUS Because Lions could only evolve prides and manes where there was space and the herds of large animals to support them, Lions are an appropriate symbol for conservation in Africa. Their presence is also the indicator of a self-sustaining community of large grazers. With wild grazers progressively being replaced by domesticated ones, the Lion has had to be eliminated. This was achieved in both N and S Africa 100 years ago. This century has seen continuous extermination across tropical Africa, with rapidly accelerating decline since publication of the first edition of this guide. The tsetse belt, a vast area once closed to livestock because of trypanosomiasis, was formerly the main refuge for the Lion and antelopes outside the national parks. New prophylactics now permit herds of cattle to occupy tsetse regions. This expansion by livestock has been so rapid and on such a scale (often without formal sanction or recognition) that its impact on the Lion is largely unknown. Its overall outcome can hardly be in doubt. Before long the Lion will survive only in the largest national parks and reserves.

LEOPARD *Panthera pardus*



Leopard

OTHER NAMES Fr. *Panthère*. Ger. *Leopard*. Swah. *Chui*.

MEASUREMENTS HB 1.04–1.40m (♀), 1.3–1.9m (♂). T 600–1,100mm. W 50kg (28–60kg) (♀), 60kg (35–90kg) (♂).

RECOGNITION A large cat with numerous, black and brown rosettes on back and upper limbs but single, solid spots on face, lower limbs and underside. Ground colour varies from pale cream (and widely spaced rosettes) in dry Somali region to deep orange or tawny brown with variably sized and spaced rosettes. Darkest forms from upland Ethiopia and Rwenzori. Commonest indications are tracks, faeces and a rasping call (over a dozen inhaling-exhaling sawings, repeated around dusk and dawn or at night).

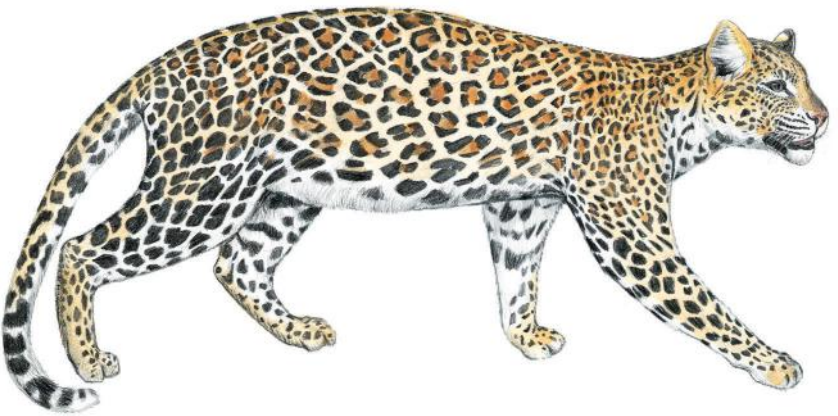
GEOGRAPHIC VARIATION In spite of very distinct regional morphs all continental populations show intermediate intergrades. The only exception was Zanzibar I. where 'founder effect' established a unique population with very numerous, very small rosettes. (The Zanzibar government deliberately exterminated this beautiful form by paying bounties for animals regarded as 'vermin'). *P. p. pardus* (continental Africa), *P. p. adersi* (Zanzibar I., extinct AD 2000).

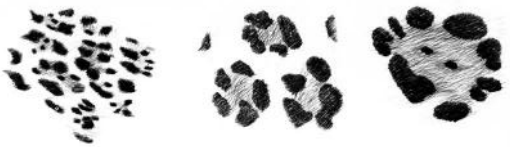
DISTRIBUTION Most of Africa (excluding the Sahara desert) with former distribution beyond, including much of S Eurasia. Now exterminated from N Africa and the greater part of South Africa.

HABITAT Leopards depend on broken terrain and heavy vegetation as stalking cover and as refuge from Lions, hyaenas and humans. They are rare or absent from wholly arid areas.

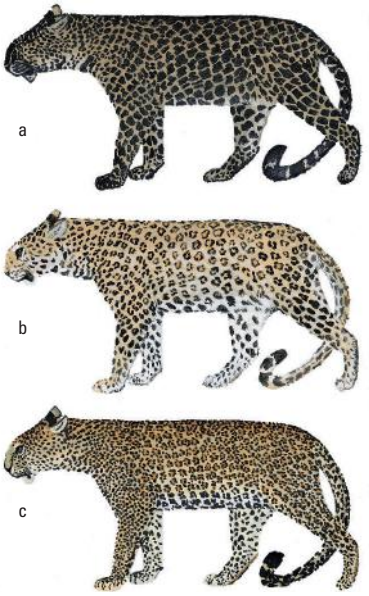
FOOD Mainly small to medium-large mammals, but very diverse foods are taken. Even in an area with numerous antelopes of all ages and sizes a high proportion of Leopard scats contain rodents, birds and arthropods (in one sample only 12% contained the remains of large antelopes). Overall, Leopard diets reflect what can be most easily caught close to the margins of thick cover. Local and individual tastes also develop, with individual Leopards regularly targeting particular prey species, such as hyraxes, ostriches, jackals, dogs or porcupines. Although well able to kill large antelopes, Leopards prefer prey no heavier than themselves. The weight of food taken at a time ranges between 8 and 17kg.

BEHAVIOUR The ranges traversed by Leopards vary from 9 to over 63km^2, but defended core areas are much smaller. They visit most of their home-range very regularly, walking about 25km a night (up to 75km if disturbed). At various land-marks, especially path intersections, they may drop faeces, spray urine or scratch tree trunks with their claws. Vocal advertisement by rasping is also





Three-tone patterning on Leopards.
Left: Two lighter toned areas balanced out by scattered clusters of small black spots. *Centre:* Rosettes consisting of black spots regularly dispersed around medium tone. *Right:* 2, 3 or 4 lesser rosettes sometimes coalesce to form larger, Jaguar-like rosettes.



Leopard morphs: (a) Ethiopian; (b) Somali; (c) Zanzibar.

frequent in areas with many Leopards. Female ranges may overlap parts of those of several males, and vice versa. Pairings are ephemeral and females raise their young alone. Gestation is 90–112 days. Up to six young are born in a cave, burrow or dense thicket where they remain hidden for about 6 weeks. Eyes open at 1 week of age and they suckle for 3 months, gradually taking more and more of the meat brought to them by their mother. They become independent before 2 years, at which time they mature sexually. They are known to live for more than 20 years.

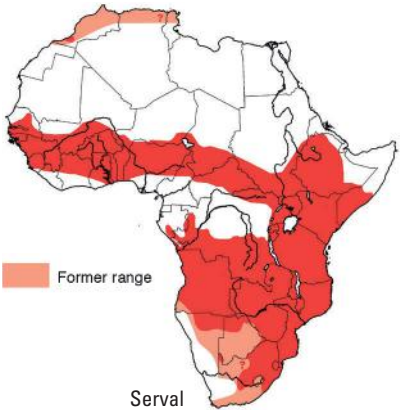
ADAPTATIONS The Leopard's coat is supreme camouflage. The larger the animal the less easy it becomes for it to imitate a specific background. The Leopard's pattern therefore must average out the light and shade in its immediate settings. Tropical Leopards not only need shade, they must anticipate prey, intruders and enemies, as well as escape mobbing by birds or monkeys. The Leopard's coat is a geometric abstraction that breaks up the tones of dappled shade into broad averages of area and contrast.

STATUS In spite of intense persecution Leopards survive in many parts of tropical Africa and they are sometimes even able to re-colonise lost ground. Nonetheless, Leopards have disappeared from many regions, especially in North, West and southern Africa. In spite of Leopards being listed in CITES Appendix I (which prohibits exploitation), the demand for their skins in the 1970s was estimated to fuel an annual off-take of some 50,000 Leopards in Africa; at present, skins continue to be illicitly traded for high prices. The practice of poisoning all predators is spreading wherever there is livestock. While the Leopard is unlikely to become extinct as a species in Africa as a whole, several unique morphs (notably those in Somalia, Rwenzori and, formerly, Zanzibar) are currently endangered or extinct.

SERVAL *Leptailurus serval*

OTHER NAMES Fr. *Serval*. Ger. *Servalkatze*. Swah. *Mondo*.
MEASUREMENTS HB 670–1,000mm. T 250–380mm. W 6.0–13.5kg.
RECOGNITION A tall, spotted cat with very large ears, a small muzzle and shortish tail. In SW Uganda and E DR Congo finely freckled Servals can be nearly as common as the more widespread, bold-spotted morph (both occur in the same litter). Various forms of brownish melanic Serval through to all-black animals also occur, especially in or near mountainous areas.
GEOGRAPHIC VARIATION None, but freckled morphs have been mistakenly assigned to distinct species *L. brachyura* and *L. servalina*.
DISTRIBUTION Once widespread in all savanna areas of Africa, including the N African coast, but now exterminated from most densely populated areas. Naturally absent from the rainforest blocks and open desert.
HABITAT Grass savannas, subalpine and montane mosaics of moorland, forest and glades. Abundant along the margins of forest galleries, reedbeds and marshes, also in fallows of cultivation mosaics.

Serval male in mild threat posture.

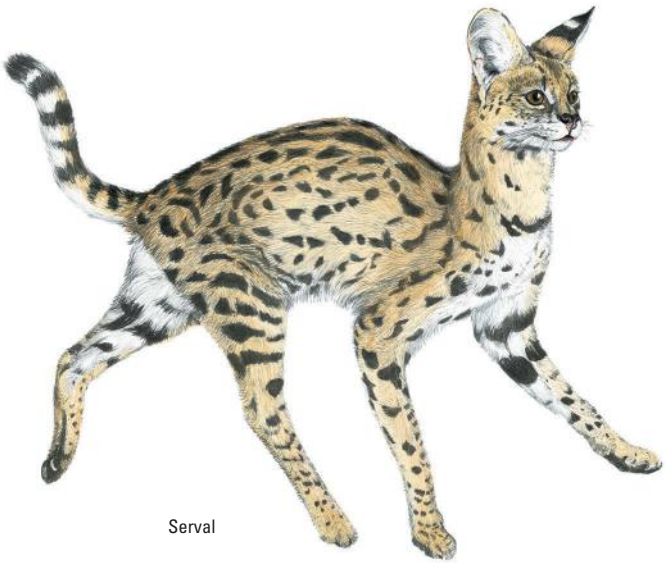


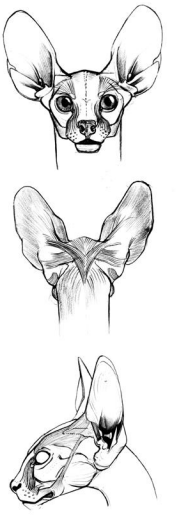
Serval

FOOD Wide range of small mammals, birds, reptiles and insects; occasionally fruits. Grass-dwelling rodents are the main prey and times when local rodents are active strongly influence Serval hunting patterns. Where diurnal species, such as grass rats (*Arvicanthis*), are dominant the Serval hunts during the day; nocturnal rats, such as *Otomys* and *Dasymys*, require more crepuscular or night hunting. High leaps or springs, with a powerful downward strike by the claws, are employed against larger prey, such as young antelopes and snakes as well as rodents. Loose, well-splayed toes with sharply curved claws also assist the long, slender forearms in reaching down burrows or tree hollows to extract rodents or nestlings. Fish and frogs are commonly caught by similar vertical strikes or by scooping and catching in mid-air. The Serval plucks birds and hares, and typical 'play' or tossing often changes imperceptibly into deliberate plucking. It will cache parts of a larger prey, returning later to uncover and consume it. Prey is sometimes disembowelled and the viscera left uneaten.

BEHAVIOUR The Serval has small, defended core territories but shares much larger areas (from 2 to 30km^2) with other Servals. Both sexes mark the home-range with urine squirts and employ a high-bounding display during rare territorial encounters. Female advertise their oestrus with loud, yowling cries, urine squirts, flank-rubbing and vertical tail quivers. Gestation lasts 67–77 days and the one to four young are born, blind and helpless, with very short tail and ears (growth of the ears is astonishingly rapid). The kittens are hidden in long grass, thickets or rock crevices and may be moved frequently. Although young may begin to eat prey brought to them by the mother after they are 4 or 5 weeks old, she suckles them up to 6 months. Young become independent at 1 year, by which time male offspring are driven off but females may be tolerated. Sexual maturity is reached at 2 years and animals live for between 13 and 20 years.

ADAPTATIONS The Serval, relatively, has the longest legs of all cats. These are not for fast running but to gain elevation for hunting in tall grass. Although the Serval can walk up to 6km a night when prey is scarce, it normally remains in a small area and travels an average of 2km. It is capable of

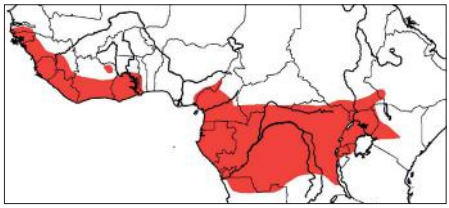

Serval


Serval, myology of ears

fast, agile dashes into dense cover if disturbed by a larger carnivore but is unable to sustain flight, preferring to hide and crouch. Its tall-grass habitat not only demands vertical leaping and striking at prey, but has shaped its typical greeting and threat displays. The head is repeatedly raised and lowered on the long neck and animals may stand on tip-toe, with highly arched back and tail. In aggression barks and growls are interspersed with forward strokes or a long-reaching, downward slash with extended claws. The primary function of the tall, vertically set ears is to act as sound funnels which allow an accurate fix on prey. For this the detector must gain maximum elevation and the Serval is an efficient hunter in tall grass (very high ratios of kills to strikes have been observed). Unlike the larger cats, where one large prey may be the outcome of several attempts, the Serval catches many small animals with less effort wasted.

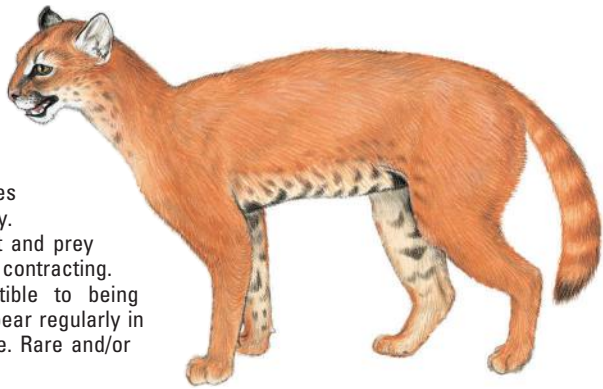
STATUS Although still widespread and common, the Serval's disappearance from very large areas of its former range in North and southern Africa and its known vulnerability to dogs suggests that its decline and demise may be rapid in areas of dense settlement. Pelts are a further inducement for poachers and hunters.

AFRICAN GOLDEN CAT *Profelis aurata*



African Golden Cat

OTHER NAMES Fr. *Chat doré*. Ger. *Goldkatze*.
MEASUREMENTS HB 610–1,015mm. T 250–370mm. W 6.2–14kg (males heaviest and 18kg reported).
RECOGNITION A powerful cat with even limb proportions, a heavy muzzle and small, black-backed ears. Adult sizes are very variable, as is the proportion of the tail. Colour and pattern are also varied, the background colour from red or yellow to smoky grey. All animals have boldly spotted bellies and inner limb fur, but those from E Africa and Senegal are otherwise unspotted, while those from Sierra Leone to Ghana are always spotted. In central Africa both spotted and unspotted ones occur. Spots range from fine freckles to large rosettes, from faint to bold, and from partial to overall. Before all this variation was understood, many races and species were described. Captive specimens are known to have changed from grey to red and vice-versa and this may also occur in the wild.
DISTRIBUTION Forested regions of tropical Africa.
HABITAT Mostly in lowland forest zone; also in secondary vegetation along rivers in outlying areas and at high altitudes in several mountainous areas in moorland, bamboo and montane forest.
FOOD The remains of duikers, monkeys, rodents and birds are commonly found in African Golden Cat faeces. In the Rwenzori Mts, it feeds mainly on rats, hyraxes and red duikers. Francolins and guinea-fowl are also commonly taken.
BEHAVIOUR Nothing has been published on its social life but frequent sightings in restricted localities imply regular routines and smallish home-ranges. Females may mature sexually while still of very small size. The young are well concealed. Nothing has been published on breeding.
ADAPTATIONS The longer, heavier jaw of the African Golden Cat implies larger, stronger prey than that of Caracals and Servals. Duikers in particular are very strong, powerfully built antelopes and are known to be regular prey.
STATUS Little known but habitat and prey populations are known to be contracting. They are particularly susceptible to being caught in snares. Cat skins appear regularly in markets all over the forest zone. Rare and/or vulnerable.

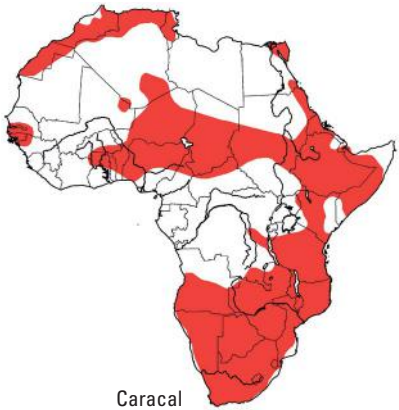


Polymorphic coat patterns in African Golden Cat (spotted morphs more common in West Africa, unspotted morphs more common in East Africa).

CARACAL *Caracal caracal*

OTHER NAMES Fr. *Caracal*. Ger. *Wüstenluchs*. Swah. *Simba mangu*.
MEASUREMENTS HB 620–910mm. T 180–340mm. W 8–13kg (♀), 12–19kg (♂).
RECOGNITION A large cat whose colour varies by region, age, stage of moult and wear and tear, but generally with a reddish-fawn coat variably frosted with a fine grey freckle. It is sometimes melanistic. The muzzle is exceptionally short and small for such a tall cat but powerful jaw muscles underlie the broad cheeks and rounded face.
DISTRIBUTION All the drier woodlands, savannas and steppes of Africa and Arabia to NW India.

Well distributed around the margins of the Sahara, common in Somali and Kalahari regions and scattered in pockets of drier country across central and E Africa.



Caracal

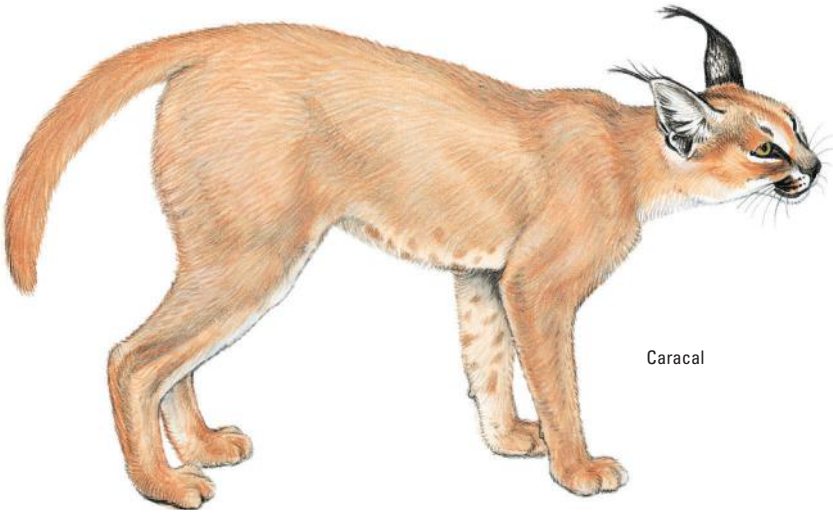
HABITAT Plains and rocky hills in country with a short wet season and limited grass cover. *Acacia* and *Commiphora* woodlands, thickets and Karoo scrub are preferred. The Arabic name, 'rock cat', reflects the animal's preference for jebels and stony outcroppings.

FOOD Depending on the locality, hyraxes, hares, small monkeys, antelopes and rodents make up the bulk of the diet. Birds such as partridges and doves are locally and seasonally important. Reptiles and fruits may also be occasional foods. The Caracal stalks its prey to within range of its prodigiously long and fast bounds or spring, which is powered by disproportionately long and muscular hindlegs. This can take it several metres up into a tree or over rocks. Even eagles and ostriches have been recorded as quarry. Difficult prey may be repeatedly raked with the hindlegs until subdued.

BEHAVIOUR Mostly solitary, the Caracal forms pairs or small mother–young groups for the period of mating and rearing. It has a typical cat repertoire of growls, spits, hisses and miaows but also a highly distinctive coughing call during breeding seasons. The breeding season may be during the spring in temperate Asia and forms an extended peak during the South African summer. Up to four young are born in a burrow, cave or thicket after a 62- to 81-day gestation. Eyes open by 9 days, meat is being taken by 1 month and lactation ceases by 4 months. The young mature fast and are wholly independent at 1 year of age.

ADAPTATIONS The strongly patterned face and ears of the Caracal stand out from an otherwise well-camouflaged body. The ears are a highly mobile signalling device. The long tufts on the ear tips may help to enhance hearing but also serve to emphasise the direction and movement of the ears and head.

Caracal facial expressions



Caracal

When meeting, and while still at some distance from each other, Caracals make ritualised head and ear movements, or 'flagging', that is thought to semaphore information on status, identity and intentions.

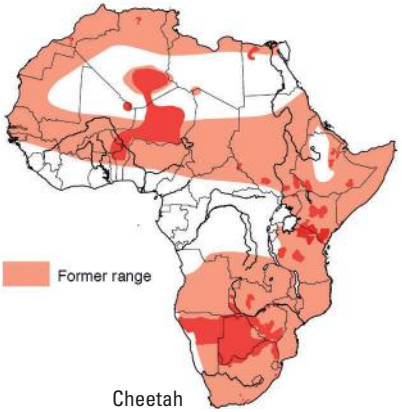
STATUS The Caracal has proved better able to withstand persecution than many other cats and carnivores. It is known to survive in many areas of North and southern Africa in spite of being rare and seldom seen. Not endangered.

CHEETAH *Acinonyx jubatus*

OTHER NAMES Fr. *Guépard*. Ger. *Gepard*. Swah. *Duma*.

MEASUREMENTS HB 1.1–1.5m. T 650–900mm. W 50kg (35–65kg).

RECOGNITION A very tall, slender cat with evenly spaced, circular spots all over a tawny-cream background. The face is notable for its rounded verticality, a structural peculiarity emphasised by prominent black 'tear stripes' that link eyes and mouth. Although the small ears have black and white markings behind, they are less conspicuous than the expressive eyes and mouth. Very young Cheetahs have extraordinary colouring: dirty white above, near black below. Underparts lighten and the spots emerge before they are 2 months old but the mantle of pale fur disappears more slowly and traces of the mantle are still present after animals are 1 year old.

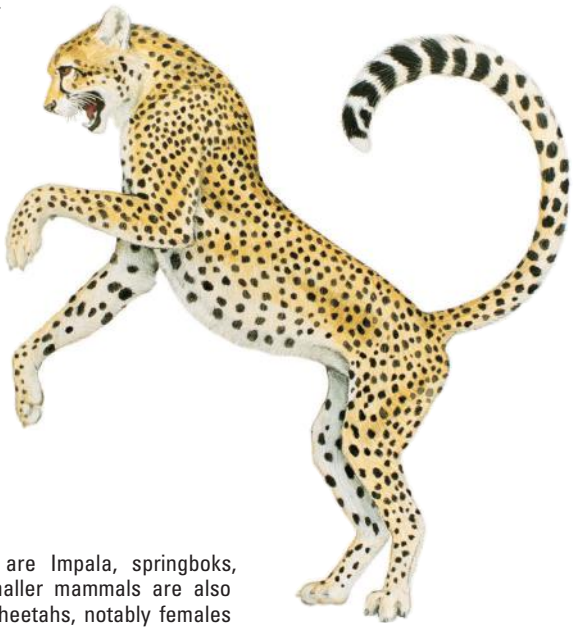


Cheetah

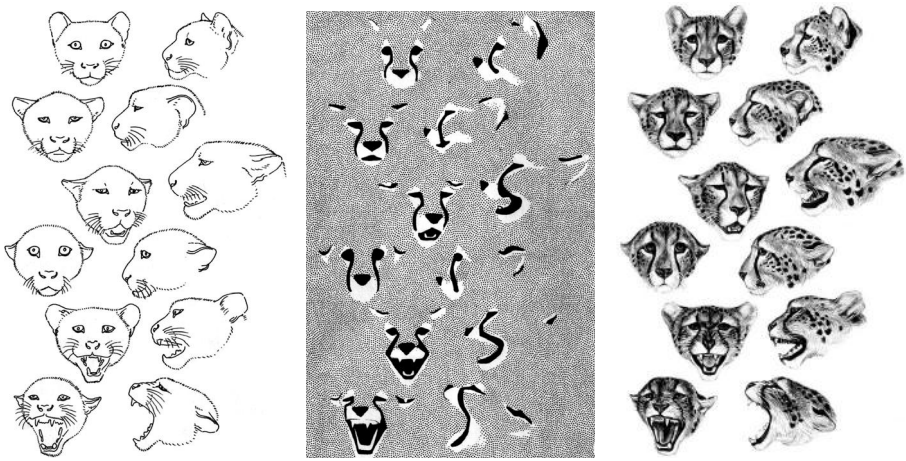
GEOGRAPHIC VARIATION All Cheetahs have been shown to be very similar genetically. This suggests supposed subspecies are unlikely. As with other spotted cats, there are occasional mutants, some totally without spots, melanistic ones, white ones with bluish spots and blotched or marbled morphs that were once described as 'King Cheetahs' and given the name *Acinonyx rex*. This morph is commonest in south–central Africa.

DISTRIBUTION The Cheetah once ranged through Africa and the Middle East across to Tadjikistan in the north and India in the south-east. Throughout its range outside Africa it has been exterminated or is on the point of extinction.

HABITAT Any large population of small or medium-small ungulates can support the Cheetah if the vegetation is not too dense or the ground too broken. Patchy cover is most favourable but the Cheetah can also survive on dry, open plains. It formerly penetrated deep into the Sahara from refuge areas to the north and south. Although extinct in the Mediterranean N Africa, it is still recorded occasionally in the vicinity of the Aïr and Hoggar-Ajjer Mountains.



FOOD The 'staple' species taken are Impala, springboks, gazelles and Kob. Many other smaller mammals are also taken but less frequently. Single Cheetahs, notably females



Cheetah. *Right*: 12 heads with diverse facial expressions. The same 12 heads in outline (*left*) and showing tonal contrast (*centre*).

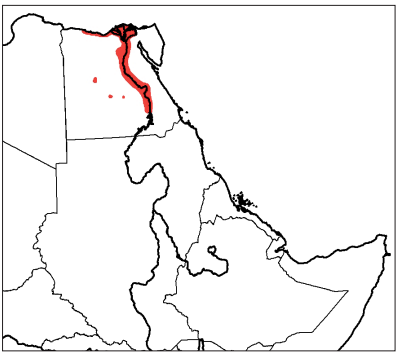
(and the minority of solitary males) hunt smaller prey and kill less frequently than male groups. Two or more females have been known to tackle much larger animals, up to the size of a zebra or young buffalo, but this is rare. The Cheetah prefers to stalk to within less than 50m before racing out at about 60km/h. At its fastest, however, a Cheetah may reach 112km/h but is quickly exhausted. An individual can consume 14kg at one sitting and groups of four have been seen to finish an Impala carcass in just over 15 minutes. Many groups kill daily. The Cheetah is a fast, frequent and efficient killer, and a speedy swallower; such adaptations help to counter loss to a host of scavengers and thieves, from vultures and hyaenas to humans.

BEHAVIOUR While two or three males often form lasting associations that jointly defend cores of shared territory (40–80km^2) the majority of adult Cheetahs (all females and some males) live in home-ranges that are much larger (50–1,000km^2). Females are mated by males that live within their own range or by wanderers. After a 3-month gestation, the blind, helpless cubs are born in long grass, in thickets or in a temporary 'borrowed' burrow. The young open their eyes at 4–14 days and are frequently carried to fresh hiding places by the mother. The cubs' first meat is eaten before they are 1 month old. Cubs vary a great deal in the length of time they remain dependent on the mother; some stay with her for 2 years, others are on their own at just over 1 year. Territories and preferred routes are marked with sprays of urine, faeces and, occasionally, by claw-raking. These markings are most often made near regularly used observation points (termitaries, rocks, leaning trees) or at path junctions. The Cheetah purrs in greeting known individuals but the most striking contact call is an explosive yelp that can carry for 2km. Juveniles make a 'whirr', or fast growl, which may rise to a squeal or subside to a rasp during fights over a kill. Chirps, hums, purrs and yelps are unique to this cat, which can be very vocal in its rare social encounters. Animals mature sexually and can have cubs of their own at about 2 years. Captive specimens have lived for up to 16 years.

ADAPTATIONS The Cheetah's skull is extensively modified to allow the jaws to serve as a clamp capable of maintaining a tight throttle hold for up to 20 minutes, until the prey has died of suffocation. The nasal passages are exceptionally large to let the Cheetah 'pant' through the nose while maintaining its vice-like grip. The clamping action is helped by a steepened angle to the face that has raised the top of the skull and eyes.

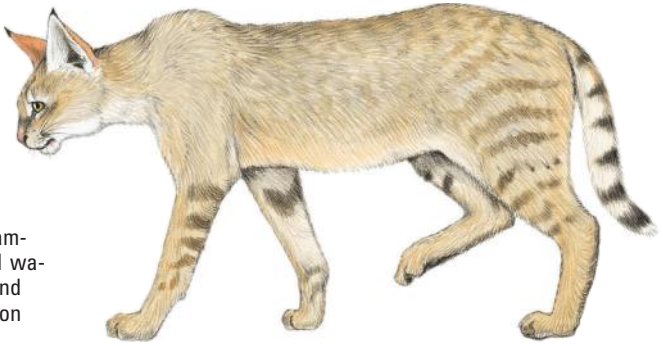
STATUS The Cheetah is represented in many very scattered national parks. Nominally protected by CITES and the African Convention. In spite of improved legal protection, its overall range has shrunk and continues to shrink as livestock replaces wildlife. Almost all African countries outlaw the killing of the Cheetah and trade in its skins, and legislation is thought to have slowed direct destruction of the Cheetah (a single furrier in New York was found with nearly 2,000 skins in 1972). Fears have also been expressed that a loss of genetic diversity could render the Cheetah vulnerable to pandemics.

SWAMP CAT *Felis chaus*



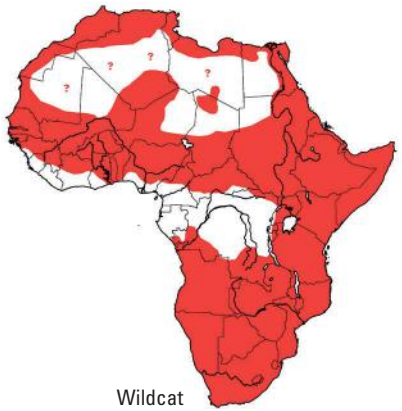
Swamp Cat

OTHER NAMES Jungle Cat. Fr. *Chat des marais*. Ger. *Rohrkatze*.
MEASUREMENTS HB 600–900mm. T 200–350mm. W 7.0–13.5kg.
RECOGNITION A large-bodied, long-legged cat with a shortish, banded tail and large, pointed ears. The colour is pale ochre, with grey tints and indistinct striping on the hindlimbs and darker bands below the elbow.
GEOGRAPHIC VARIATION *F. c. nilotica* (lower Nile Valley).
DISTRIBUTION An Asiatic species just intruding into Africa (former Saharan records are due to mistaken identification).



HABITAT Known mainly from wetlands throughout its South-East Asian and Indian range. In Egypt it lives in reedbeds and low grassy valleys, mainly near settlements.
FOOD Mainly small mammals, migratory birds and waterfowl, also reptiles and frogs. It is dependent on water.
BEHAVIOUR An exceptionally hardy species that can breed and survive exposure in open marshlands. Two to five young are born after a 66-day gestation, suckle for 2 months, are independent by 5 months and sexually mature by 18 months.
ADAPTATIONS Unusually for a cat, the Swamp Cat is a good swimmer and hunts in water-logged swamps. Its fur resists soaking and dries out fast. Primarily nocturnal.
STATUS Uncertain but evidently precarious in Egypt. Very restricted habitat, wholly enclosed by dense human settlement. Lining the banks of the Nile with stone walling has further eroded suitable habitat for this species.

WILDCAT *Felis sylvestris*



Wildcat

OTHER NAMES Fr. *Chat ganté*. Ger. *Wildkatze*. Swah. *Paka mwitu*.
MEASUREMENTS HB 450–730mm. T 200–380mm. W 2.4–6.5kg.
RECOGNITION This species closely resembles a domestic cat (of which it is the direct and recent ancestor), with a grey or buff ground colour and warmer tints on the face, back of the ears and on the belly. Darker types are found in more humid areas. Tracks, typical cat faeces and fine scratch marks are indirect signs. Plain gingery backs to the ears and long legs distinguish the Wildcat from domestic cats.
GEOGRAPHIC VARIATION Individual variation (especially lighter and darker morphs) superimposed on

Wildcat

regional differences and domestic crosses make definition of subspecies difficult and their usefulness questionable.

DISTRIBUTION Most of Africa except the more extensive areas of desert and rainforest.

HABITAT Woodlands, savannas, grasslands and steppes. In more exposed areas Wildcats may shelter in and even share the dens of other animals. Litters are born in such retreats under dense grass, in hollows, crevices or tangles.

FOOD Mainly rats, mice and small mammals up to the size of a hare or very small antelope. Birds (especially gallinacaeous ones) and, less frequently, reptiles, frogs and insects are also taken. Wildcats traverse known hunting grounds slowly and silently, alerted to prey by hearing or sight. Prey is approached with a gliding, ground-hugging run, after which they inch forward until they can strike (within about 1m). Most hunting takes place in the early morning or evening. Sometimes a cat may hunt within sight of another and drift in the same direction as its mother, mate or sibling (but most hunting is solitary).

BEHAVIOUR 'Rodent seasons' or periods of prey abundance (in the rains) may provide the basis for breeding peaks in Wildcats. A single male's range tends to overlap those of several females. The latter defend the core of their range, especially when with kittens. Males spray posts with urine and leave less obvious claw scratch-marks and cheek-rubbings. Gestation is 56–69 days. Two to six young are born helpless and blind. Mobile by 1 month, they are independent by 5 months and sexually mature by 1 year.

ADAPTATIONS The wide ecological and geographic range of this species is due to the fact that it is small enough to subsist on insects for periods, yet strong enough to take prey of its own size.

STATUS Generally rare although widespread and locally common. Prone to hybridising with domestic cats and a frequent victim to dogs. In more exposed areas Wildacts are commonly taken by eagles and larger cats.

BLACK-FOOTED CAT *Felis nigripes*

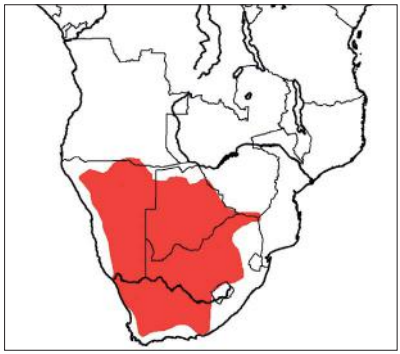
OTHER NAMES Fr. *Chat à pieds noirs*.
Ger. *Schwartzfusskatze*.

MEASUREMENTS HB 370–520mm. T 140–200mm. W 1.0–2.4kg.

RECOGNITION A small, pale tawny cat with very bold dark spots and prominent rings on the limbs, and a rather short tail. The margins of the eyes, ears and mouth are white, as is the underside. The nose is very small and the pointed ears are widely spaced.

GEOGRAPHIC VARIATION *F. n. nigripes* (Kalahari): paler spots. *F. n. thomasi* (S Karoo): black spots.

DISTRIBUTION Arid regions of the Kalahari, Karoo and W Cape.

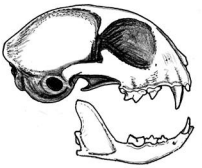


Black-footed Cat

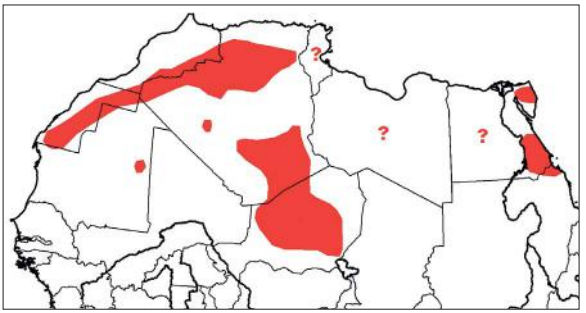
HABITAT Hunt in open, sandy country but keep close to thickets, termitaries or clumps of grass where they can make a rapid retreat. The exact requirements for this species are still unknown, and its distribution is very patchy.

FOOD Mainly gerbils and bush-rats, sengis and birds; spiders, insects and reptiles are probably more marginal foods. Black-footed Cats can live without water.

Black-footed Cat

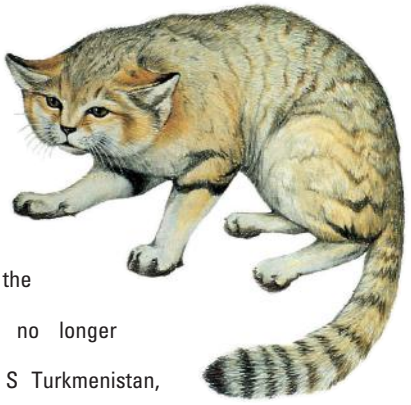


BEHAVIOUR Extreme caution and strictly nocturnal habits have ensured that these cats are very seldom seen but they are also naturally rare. Furthermore, they are intractable and ill-suited to captivity or zoo-breeding. May emerge 2–3 hours after dark but occasionally during the day. Records suggest summer (November–December) breeding. Up to three young are born after 67–68 days' gestation.
ADAPTATIONS A southern relative of the Sand Cat with three different hunting styles, namely flush, stalk and ambush, adapted to circumstance and type of prey.
STATUS Little known. Generally acknowledged as rare.



Sand Cat

SAND CAT *Felis margarita*



OTHER NAMES Fr. *Chat des marais*. Ger. *Sandkatze*.
MEASUREMENTS HB 390–48mm. T 220–350mm. W 1.5–3.4kg.
RECOGNITION A very small sandy-yellow cat with greyish freckling on the flanks, shoulders and forehead. Brown stripes on very young cats become faint gingery markings on adults but all have bolder markings around the elbows and tail tip. The ears are very widely spaced and can be deflected into a horizontal, downward orientation. The fur is dense, fine and woolly. The canines are exceptionally long for the animal's size.
GEOGRAPHIC VARIATION Three named subspecies, no longer recognised.
DISTRIBUTION Sahara Desert; also from Arabia to S Turkmenistan, Uzbekistan and Baluchistan.
HABITAT Desert areas with gerbil colonies, both sandy and rocky. It digs dens in deep sand beneath desert bushes.

FOOD Mainly gerbils and lizards, which are skilfully caught at night. However, attempts at catching birds appear inept. The Sand Cat gains most of the moisture it needs from prey and becomes torpid during the day in its deep burrow, probably in order to conserve water.
BEHAVIOUR By following the contours of the ground the Sand Cat escapes the attention of both prey and predators. Early winter births in Arabia suggest the three or four kittens may benefit from cooler, moister conditions in winter and spring.
ADAPTATIONS Dense fur on the soles of the feet probably improves purchase on soft sand. The horizontal setting of the ears may help the cat to pick up the subterranean sounds of its prey.
STATUS Very widespread range but may be locally extirpated by feral cats and dogs and by introduced diseases and parasites. Although apparently rare, unlikely to be endangered.

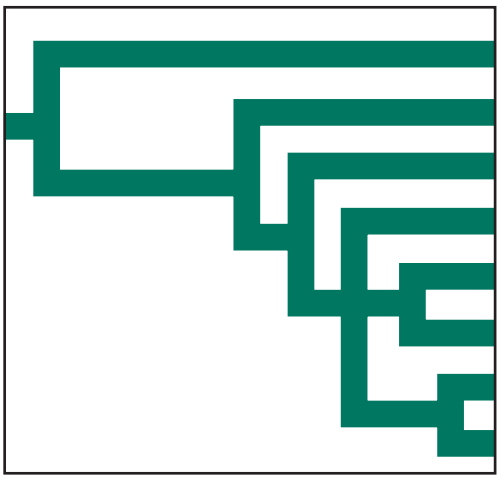
GENETS AND CIVETS VIVERRIDAE

African Civet	*Civettictis civettica*
Oyans	*Poiana* (2 species)
Genets	*Genetta* (15 species)

Viverrids are to carnivores what lemurs are to the higher primates. Civets in particular are modern, very rough approximations of what some early carnivores looked like (but not genetically). Civets are almost wholly terrestrial; large, coarse-furred animals, with blunt claws fixed in short, dog-like pads. The predominantly arboreal genets have soft fur, retractile claws, and a spotted or blotched coat pattern.

Civets are common to both Eurasia and Africa and represent the oldest viverrid lineage. With ancestor(s?) probably entering Africa later (in the late Miocene), African oyans and genets radiated here, the latter very extensively. It has been suggested that the most conservative living lineage of genets (*G. abyssinica* and *G. thierryi*) emerged about 8.5 mya. Today both species (in common with most other genets) are relatively rare, of restricted distribution, or specialised for some localised niche (for *G. johnstoni*, forest insects in Upper Guinea, for *G. piscivora*, angling for fish in Limbali forest). In striking contrast to such semi-relictual provincials, the two most recently evolved lineages, *G. genetta* + allies and *G. maculata* + allies, are very common and have extensive ranges.

Servaline Genet, facial expressions

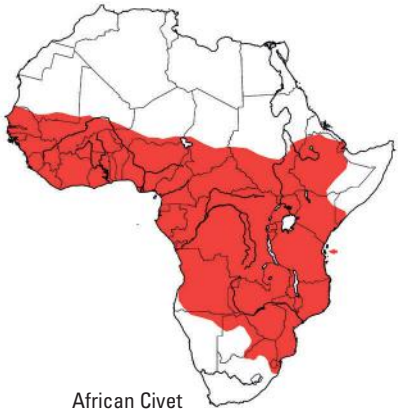


Tentative phylogenetic tree for African Viverridae (after Gaubert & Veron 2003).

The viverrid radiation in Africa is mainly tropical. Rainforests of the centre–west realm provide most of the special genet niches. Although a majority are forest-dwelling, the most successful viverrids span almost all types of wooded habitats. They are solitary foragers but some form short-lived family associations.

Scent is their most fundamental mode of communication and all species employ glandular secretions to regulate contacts and behaviour. The civets' perineal glands are the best known. This species' secretions are so copious and durable that they once provided the perfume trade with a valuable fixative for floral scents (civet is still used for perfumery in south and west Asia).

AFRICAN CIVET *Civettictis civetta*


African Civet

OTHER NAMES Fr. *Civette d'Afrique*. Ger. *Afrika Zibetkatze*. Swah. *Fungo*.
MEASUREMENTS HB 680–950mm. T 400–530mm. W 7–20kg.
RECOGNITION A shaggy, low-slung, dog-like animal with an ornate pattern of bands and blotches on body and tail, black limbs and a boldly marked face mask with pale forehead, white muzzle and black eye patches. The hair is coarse and loose and a crest extends from forehead to tail tip. The African Civet is mainly nocturnal. Its normal gaits are either a slow, tentative, low-headed walk or a more directed, steady trot. It makes very conspicuous dung middens called 'civettries', strongly scented with anal gland secretions. Quite independently, it scents landmarks in territories with large perineal glands. It is normally silent but growls very deeply and coughs explosively if harrassed or cornered by dogs or humans.
GEOGRAPHIC VARIATION Eight subspecies named. There are some regionally consistent characteristics but no clear boundaries.
DISTRIBUTION Sub-Saharan Africa but absent from southern Africa (except Transvaal), most of Namibia, Eritrea and drier areas of the Horn.
HABITAT Most abundant in forested or partly forested mosaics, in cultivated and marshy areas. It occurs only in dry, open country where dense cover grows along watercourses, around stone outcrops and in broken gullied land. In spite of its dependence on thick cover, the African Civet is most often seen trotting along established roads and pathways.
FOOD Omnivorous: vertebrates and plants (mainly roots, shoots and fruits). The African Civet is able to eat poisonous fruits such as *Strychnos*, distasteful insects such as stink locust (*Zonoceras*),

millipedes and dangerous snakes. It is also able to feed irregularly and can fast for up to 2 weeks. Prey encountered during regular circuits is either approached slowly and cautiously or disabled in a sudden, rushing lunge. Vertebrates are bitten deeply, shaken very violently, then dropped or tossed. The African Civet is known to kill prey up to the size of a hare or mongoose. Large prey is torn into pieces and bolted.

BEHAVIOUR A solitary, very intolerant animal. It is probably territorial. Up to four young are born after 60–72 days' gestation in a burrow, crevice, termitary or in dense vegetation. The young develop very fast, beginning to take solid food at 1 month and adopting adult behaviour at 5 months. Young normally 'freeze' until detected but hiss and spit when threatened. They make a soft, clucking contact note which persists into adulthood as a three-note 'duff, duff, duff' contact call or male courtship signal. Infantile miaows of distress also resemble adult female oestrus calls.

ADAPTATIONS The copious flow of secretions from the perineal glands was once harvested from captive specimens as 'civetone', a floral-scent fixative. It is smeared on landmarks throughout the home-range, especially rocks and stumps at path intersections and on the tree trunks of favourite fruiting trees. Circulates regularly over a large home-range or territory but does not have regular dens, being essentially a 'camper' that will lie up during the day in any thick vegetation or natural hollow. Frequent and copious scent marks provide a necessary orientation and spacing system. Adult males augment civetone and dung signals with urine that is squirted backwards, like a cat. Although most contacts are kept indirect and at a distance by means of scent marks, direct encounters elicit a variety of postures that are enhanced by raising or depressing the crest and body fur, thus exposing strongly contrasting patterns. The throat is frequently rubbed on objects and is boldly marked. Even as young cubs, siblings fight readily. Presumably such intolerance is broken down by appropriate olfactory and visual signals during courtship.

STATUS Widely distributed and common in spite of very frequent road kills. Not endangered.

OYANS *Poiana*

Central African Oyan	*Poiana richardsoni*
West African Oyan	*Poiana leightoni*

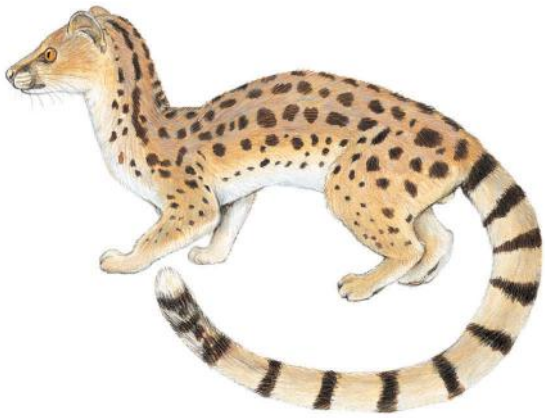
Formerly thought to be related to Oriental linsangs. Now known to be genetically allied to genets.

CENTRAL AFRICAN OYAN *Poiana richardsoni*

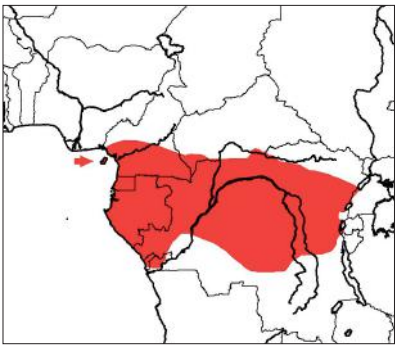
OTHER NAMES Central African Linsang. Fr. *Poiane centrafricaine*. Ger. *Centrum Afrika-linsang*.

MEASUREMENTS HB 320–400mm. T 340–400mm. W 455–750g.

RECOGNITION Resembles a very slender, small-muzzled, small-eared, long-tailed genet but differs in its dentition and skull. Round, brown spots are scattered over reddish-brown upperparts. The spine is marked by a long line of spots or dashes. The off-white underparts are unspotted. The tail,



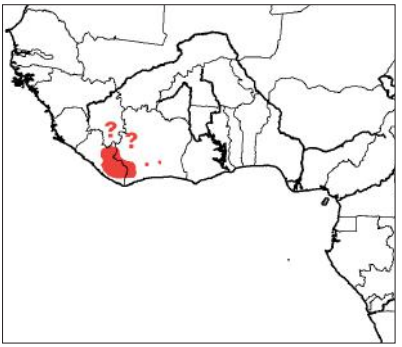
longer than the body, is encircled by 12–14 parallel-sided black rings.
GEOGRAPHIC VARIATION *P. r. richardsoni* (Bioko I.), *P. r. ochracea* (Cameroon to E DR Congo).
HABITAT Rainforests. These nocturnal, highly arboreal oyans are thought to move every few days, presumably on regular circuits, sleeping in nests during the day and rarely coming to the ground. Their precise habitat needs are unknown.
FOOD Arboreal vertebrates, invertebrates and fruits.
STATUS Capable of raising two litters a year, each of up to three young, oyans are nonetheless rarely seen and little known. Genetically, African oyans appear to be a specialised branch of the genet radiation. Widely distributed and poorly known.



Central African Oyan

WEST AFRICAN OYAN *Poiana leightoni*

OTHER NAMES West African Linsang. Fr. *Poiane d'Afrique occidentale*. Ger. *West Afrika-linsang*.
MEASUREMENTS HB 300–380mm. T 350–400mm. W (est.) 500–700g.
RECOGNITION Notable for its very long, soft-furred tail, marked with dark asymmetrical chevrons graduating to rings, this plush-coated, pale-coloured oyan has small, sometimes irregular spots that are well spaced but a continuous black-brown line runs down the spine. The underside is unspotted and pure white.
HABITAT Only known from rainforest in E Liberia and W Côte d'Ivoire, where it is reputed to live in tree crowns above 30m. Several animals may share a single, globular nest constructed of fresh green material. It is thought that these are made by the oyans and not appropriated from squirrels.



West African Oyan

FOOD Young birds, insects and plant material, including kola fruits.
STATUS This rare and interesting species shares its small and shrinking range with many other endemic animals and plants. Rare and vulnerable. IUCN: status uncertain.

West African Oyan, frontal view

GENETS *Genetta*

Ethiopian Genet	*Genetta abyssinica*
Hausa Genet	*Genetta thierryi*
Giant Genet	*Genetta victoriae*
Servaline Genet	*Genetta servalina*
Crested Genet	*Genetta cristata*
Johnston's Genet	*Genetta johnstoni*
Aquatic Genet	*Genetta piscivora*
Common Genet	*Genetta genetta*
Feline Genet	*Genetta felina*
Miombo Genet	*Genetta angolensis*
Cape Genet	*Genetta tigrina*
Blotched Genet	*Genetta maculata*
Pardine Genet	*Genetta pardina*
King Genet	*Genetta poensis*
Bourlon's Genet	*Genetta bourloni*

Genets are slender, long-bodied, cat-like carnivores, described as 'rat-like leopards' in one part of Africa. They have cat-like semi-retractible claws, a long, banded tail, soft fur, large ears and a pointed muzzle. They are spotted or blotched (occasional black morphs are also known). They have anal sacs and perineal musk glands (like civets). Normally silent, they spit, hiss, growl, purr and miaow like cats but also cough, whine and scream. They are mainly nocturnal.

Distribution is mainly sub-Saharan Africa, but one species (*G. genetta*) extends to Morocco to Tunisia, Spain, SW France and Arabia. Genets inhabit forests and all wooded habitats, including very thinly bushed valleys in desert. They are omnivorous, with marked specific preferences for either more or less vertebrates, invertebrates or plant matter. Small animals are ambushed or caught after a short stalk or fast pounce – genets are fast but clumsy killers, relying on speed and agility and cryptic colouring to catch food (and also to evade larger predators).

They are solitary except during brief courtship and for about 6 months while the young are with the mother. Ranges of males are up to 5km^2, those of females are much smaller. Male ranges overlap those of several females, and also other males. They have a well-developed spatial sense (artificially displaced genets have been recorded homing over 35km^2). Latrines and marking sites are used by more than one animal, with males mainly using their urine and females their perineal glands. Up to five young are born, blind and helpless, in a hollow or a vine tangle after about 70 days' gestation. They become independent after about 6 months and are mature and able to breed at about 1 year.

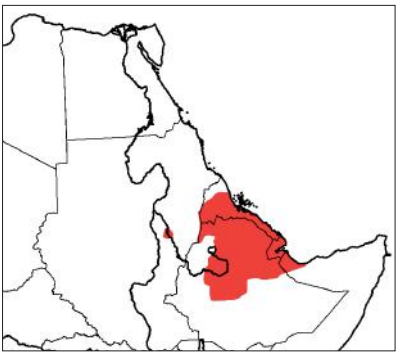
Genets bear an extraordinary resemblance to the unrelated spotted marsupial *Dasyurus* and to the Cacomistle, *Bassariscus* (a raccoon). They also resemble the Madagascan Fossa and Oriental linsangs, *Prionodon*, despite their common ancestry parting more than 20 mya. This suggests that the requirements for success in the arboreal niche is as exacting for small carnivores as it is for some primates (which are also convergent on different continents).

Several species are extremely rare and localised. Most are widespread and successful.

ETHIOPIAN GENET *Genetta abyssinica*

OTHER NAMES Fr. *Genette d'Ethiopie*. Ger. *Streifenginsterkatze*.
MEASUREMENTS HB 400–500mm. T 380–450mm. W 1.3–2.0kg.
RECOGNITION A pale, sandy genet with five black stripes running down the back. The fur is short, fairly coarse and of a uniform length. The black-tipped tail has seven or eight relatively narrow black rings. Forefeet are distinguished by the absence of fur between the digit pads and the 'palm'.
HABITAT Eritrea, Somalia and Ethiopia. Recorded from Red Sea coast to the Ethiopian highlands in dry woodlands, but its precise range and preferred habitats are not known.
FOOD Presumed to resemble other genets. Captives thrived on pet food.
STATUS Unknown (IUCN).

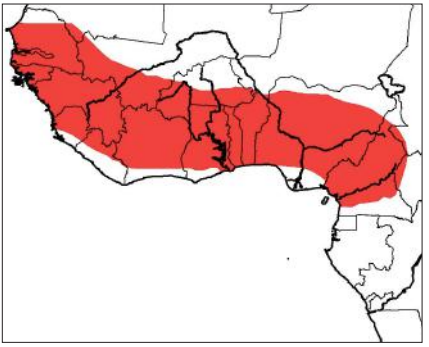
Ethiopian Genet



Ethiopian Genet

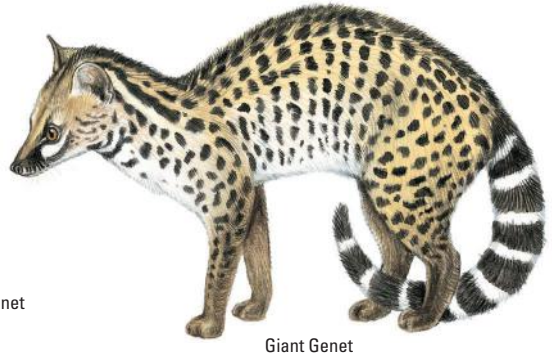
HAUSA GENET *Genetta thierryi*

OTHER NAMES Fr. *Genette de Villiers*. Ger. *Haussa-Ginsterkatze*. Swah. *Kanu*.
MEASUREMENTS HB 380–450mm. T 370–450mm. W 1.3–1.5kg.
RECOGNITION A small, tan genet with blotchy spots following linear patterns down the back, often rich reddish-orange. There is no crest and spotting is generally sparse on the face and forequarters. The long tail is black-tipped, tapered and marked by incomplete dark rings which have a rich orange suffusion near the body but become darker towards the tip.
HABITAT Sparsely distributed in drier savannas from Guinea to Cameroon. Eastern limits uncertain.
FOOD Probably as for other genets.
STATUS A rare species, poorly known.



Hausa Genet

Hausa Genet

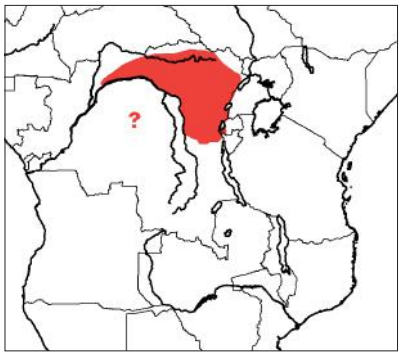


Giant Genet

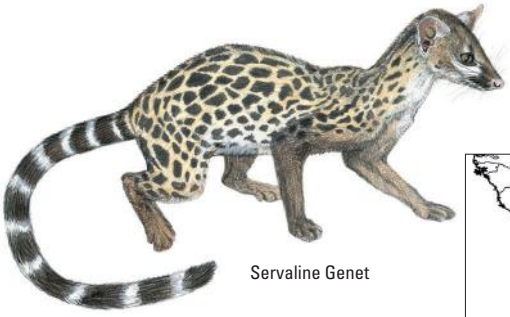
GIANT GENET *Genetta victoriae*

OTHER NAMES Fr. *Genette géante*. Ger. *Riesenginsterkatze*.
MEASUREMENTS HB 550–600mm. T 450–500mm. W 2.5–3.5kg.
RECOGNITION A large genet with dense soft fur, long legs and a fine, narrow muzzle. Black spots are very numerous (but subject to individual variation) and well distributed over the tan upperparts, off-white neck and undersides and sepia lower limbs. The tail is boldly banded in black and white and tapers near the tip.

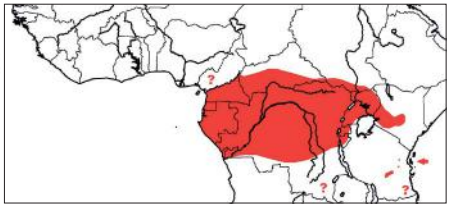
HABITAT NE DR Congo and extreme W Uganda. Very patchily distributed in rainforests at low and medium altitudes.
FOOD Not known from the wild but a captive specimen ate rats and bananas (mixed with milk and rice).
STATUS It is likely to occur in Maiko NP but while the reasons for its discontinuous distribution remain unknown it should be considered at risk.



Giant Genet



Servaline Genet



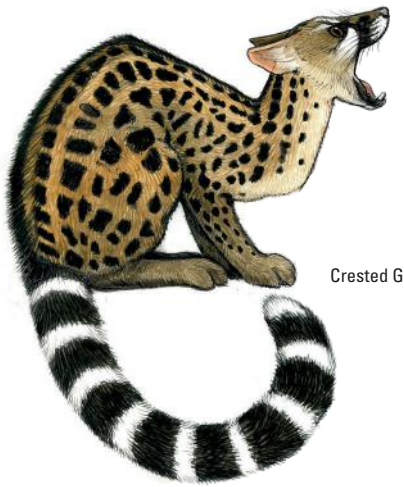
Servaline Genet

SERVALINE GENET *Genetta servalina*

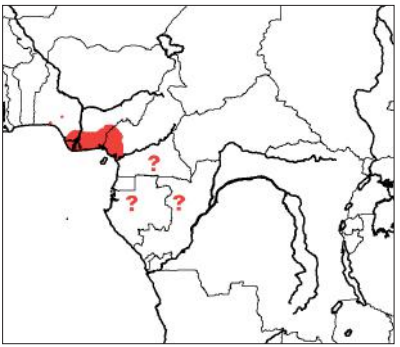
OTHER NAMES Fr. *Genette servaline*. Ger. *Waldginsterkatze*. Swah. *Kanu*.
MEASUREMENTS HB 410–510mm. T 350–485mm. W 1.0–2.7kg.
RECOGNITION A small, slender genet with a narrow face, rather long legs, very soft, dense, short fur and no dorsal crest (a short crest on the back of the neck may sometimes extend to the shoulders). Black spots are densely distributed over the body and limbs on a tan or orangey background. The tail is not tapered and its 8–12 black bands are often broader than the pale ones. It is exclusively nocturnal.
GEOGRAPHIC VARIATION *G. s. servalina* (Congo R., R. Ogooué basins, main lowland forest block), *G. s. bettoni* (montane E and central Africa), *G. s. lowei* (Uzungwa Mts), *G. s. archeri* (Zanzibar).
HABITAT A rainforest species, apparently absent from the Upper Guinea forests. Servaline Genets occur in both lowland and montane forests. They are often encountered on the ground.
FOOD Ground-dwelling rodents, tree hyraxes, birds, insects and fruits have been recorded. It is possible that birds are located from the ground and then stalked while sleeping in the trees but other foods suggest ground-foraging.
STATUS Widely distributed but poorly known (*G. s. lowei* was known from one incomplete specimen but has since been camera-trapped in the Udzungwa Mts).

CRESTED GENET *Genetta cristata*

OTHER NAMES Fr. *Genette servaline a crete*. Ger. *Haubenginsterkatze*.
MEASUREMENTS HB 490–620cm. T 430–500cm. W (est.) 2–3kg.
RECOGNITION A slender, long legged genet resembling *G. servalina* but with a distinctive, erectile dorsal crest. Black spots numerous and of linear distribution. Pale neck and chin but belly and limbs deep sepia. Tail boldly banded with slightly narrower white ands between broader black bands.
HABITAT Forests in Bight of Benin, from Niger Delta to Congo R.
FOOD A high proportion of insects and traces of vegetable matter, rodents and reptiles.
STATUS Largely unknown.



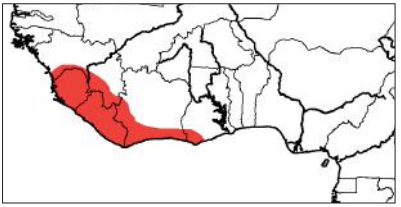
Crested Genet



Crested Genet

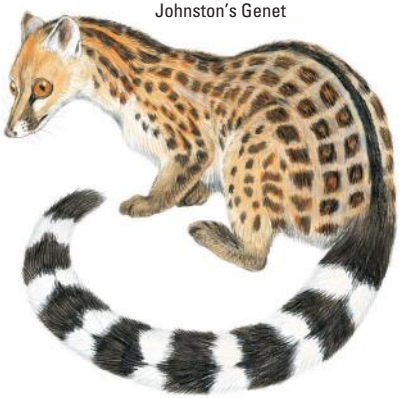
JOHNSTON'S GENET *Genetta johnstoni*

OTHER NAMES Fr. *Genette de Johnston*. Ger. *Liberia Ginsterkatze*.
MEASUREMENTS HB 400–520mm. T 400–540mm. W (est.) 1–3kg.
RECOGNITION A thickly soft-coated genet with large eyes and a fine muzzle. The upperparts are tawny with rows of spots down the flanks and back (which become larger and more regular as they approach the midline). There is a short dorsal crest. The tail is densely furred and has about 16 evenly spaced, black-and-white bands. This species has a feebler dentition than other genets.
HABITAT Known from rainforest in Liberia and Guinea (but may also occur in W Côte d'Ivoire).
FOOD Not recorded but likely to include soft-bodied insects.
STATUS Known from very few museum specimens. All genet species are intensively hunted for bushmeat and for their ornamental skins. IUCN rates this species as vulnerable.



Johnston's Genet

Johnston's Genet

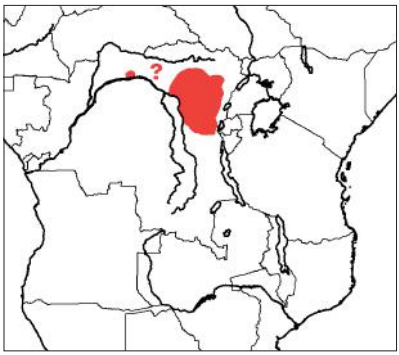


AQUATIC GENET

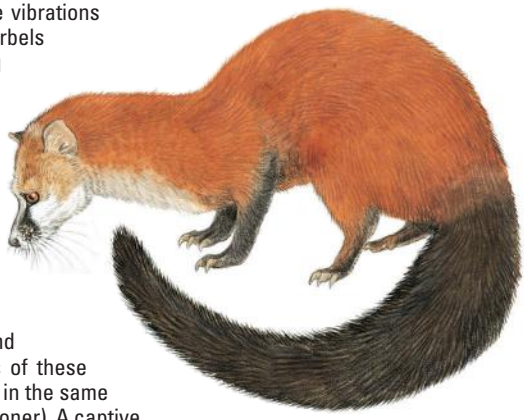
Genetta (formerly *Osbornictis*) *piscivora*

OTHER NAMES Fr. *Genette aquatique*.
Ger. *Wasserschleichkatze*.
MEASUREMENTS HB 440–500mm. T 340–420mm. W (est.) 1.2–2.5kg.
RECOGNITION A very lightly built, but densely furred genet with large, protuberant eyes, relatively small ears and a 'moustache' of conspicuous, downwardly deflected white whiskers. The body is a deep dark red (more ochraceous on the temples) while the thickly furred tail and limbs are black/brown. Throat, chin, upper lip and forecheek are white, contrasting strongly with the black/brown muzzle. The teeth resemble those of other genets but are narrower and more sharply pointed. The hands and feet are also genet-like but their undersides are largely naked and they are disproportionately small (observably inferior arboreal skills and largely terrestrial).

DISTRIBUTION Low-lying north-eastern section of the Congo basin bounded by the Congo R. and mountainous margins of the Gregory Rift.
HABITAT Shallow headwaters of streams (preferably clear and flowing over red clays and sands) within a forest type dominated by limbali trees (*Gilbertiodendron*). It shelters in fallen hollow trunks and riverside debris and is crepuscular and nocturnal.
FOOD Fish (captive specimens show no interest in small mammals, birds, lizards, frogs, insects or crabs), which are caught in the mouth with a very rapid strike. The Aquatic Genet approaches a quiet pool very slowly and gently pats the water surface. Fish are detected by sight or by the tips of the vibrissae, which are splayed in the surface layer of the water. These apparently pick up the vibrations made by fish. As the preferred prey is barbels (*Barbus*), catfish (*Clarias*) and 'talking fish' (*Synodontis*), all of which feed on insects and their larvae, it is possible that the technique not only detects fish but also attracts them.
BEHAVIOUR In spite of being able to make extremely fast strikes and to flee at speed, the Aquatic Genet's normal gait and demeanour is slow and deliberate. This is in striking contrast to the Marsh Mongoose's hunting technique (which is busy and churns up mud and water). The tracks of these two amphibious species are often found in the same places (the mongoose is generally commoner). A captive pair of Aquatic Genets exchanged very cat-like miaows and also a clucking or chuffing serial call.



Aquatic Genet

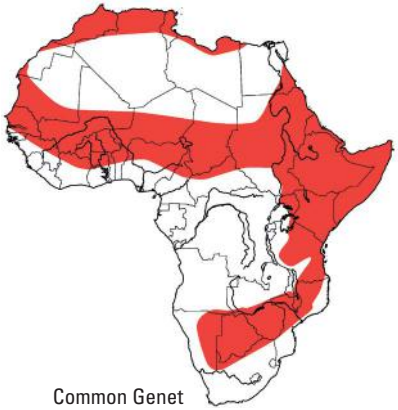

Aquatic Genet

ADAPTATIONS The 'light-touch' fishing technique used by the Aquatic Genet correlates with its extremely nimble and flexible movements. Its very gracile, slender build presumably assists speed of movement but restricts it to fish of less than 25cm in length. Its teeth are mainly suited to gripping and slicing skin, flesh and hard, bony heads. Both the fishing technique and the prey are so specific that, within its very restricted habitat, the genet is clearly able to compete with both Marsh Mongooses and piscivorous birds. Loss of patterning seems contingent upon the abandonment of arborialism. Limbali grow by preference in sandy red clays in river valleys of the NE Congo basin.
STATUS The Aquatic Genet's close link with limbali forest (thought to be an ancient and relatively stable forest type) suggests that it may also be dependent on a year-round supply of accessible small-fry fish of the right species. The species' survival is likely to depend on this forest type and on the rivers not being overly disturbed. Bakumu hunters in the heart of its range claim that it is common in several known localities but rare everywhere else. Rare and likely to become vulnerable as forest is felled and land-use practices change. IUCN classes conservation data as deficient.

COMMON GENET *Genetta genetta*

OTHER NAMES Small-spotted Genet. Fr. *Genette commune*. Ger. *Gemeine Ginsterkatze*. Swah. *Kanu*.
MEASUREMENTS HB 400–550mm. T 400–510mm. W 1.3–2.3kg.
RECOGNITION A genet with rather coarse fur and a short crest of longer fur along the spine. The ringed tail is nearly as long as the body and strongly tapered. The dark brown spots are small, numerous and linear on a sandy background. Hindfeet are pale.
GEOGRAPHIC VARIATION More than 30 subspecies have been described. Regional groups are provisional.

Common Genet



Common Genet

G. g. genetta (Mediterranean), *G. g. senegalensis* (W Africa), *G. g. dongolana* (E Africa). (*G. felina* from South Africa is treated as a sibling, but distinct species in this guide.) The Common Genet is the only genet to occur outside Africa and (including *G. felina*) is the most widely distributed species within Africa.

HABITAT A wide range of drier habitats, from seasonally arid woodlands to sparsely bushed near-desert, especially rocky, hilly country where they are able to live without water.

FOOD Varies by region, with a different spectrum of local vertebrates (rodents, birds or reptiles), invertebrates and fruits.

STATUS The European population originated from Morocco (possibly as a result of ancient introduction by humans). Not endangered.

FELINE GENET *Genetta felina*

OTHER NAMES Fr. *Genette féline*. Ger. *Felineginsterkatze*.

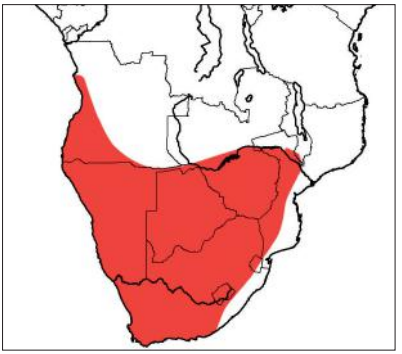
MEASUREMENTS HB 860–1000mm. T 400–500mm. W 1.5–2.6kg.

RECOGNITION Frequently treated as a subspecies of *G. genetta*, genetic isolation in temperate southern Africa has persuaded some geneticists that it deserves recognition as a species. This genet is here profiled as a 'provisional' species until further studies clarify its taxonomic status. This is a very grey species with dark grey limbs, a prominent black dorsal crest and strongly contrasting facial patterns. Black spots small and rounded. Tail evenly banded in black and white.

HABITAT Occurs from coastal Namibia to W Zambia.

FOOD Prefers rodents and birds but other vertebrates and arthropods taken.

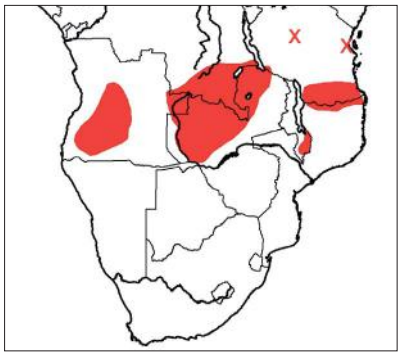
STATUS A very common and widespread species.



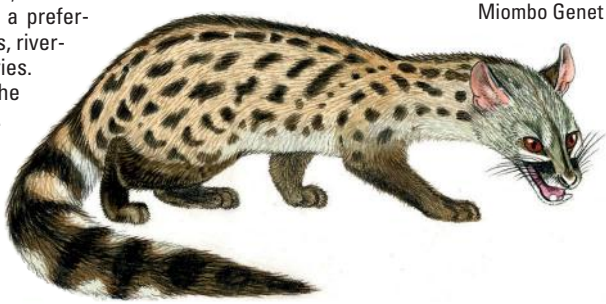
Feline Genet

MIOMBO GENET *Genetta angolensis*

OTHER NAMES Fr. *Genette d'Angola*. Ger. *Bürstenginsterkatze*.
MEASUREMENTS HB 440–480mm. T 380–430mm. W 1.3–2.0kg.
RECOGNITION A dark grey or brownish genet with a dorsal crest and irregularly spotted coat. The underside of the paws and the feet are blackish. The tail is darker ochre above and white below, with about eight black rings. The face is dark with strongly contrasting white flashes below the eyes and muzzle. Wholly or partly melanistic morphs known.
HABITAT Miombo (*Brachystegia*) woodlands from Angola to Tanzania, with a preference for the moister woodlands, riverine vegetation and forest galleries.
FOOD Rodents are likely to be the main staple; also invertebrates.
STATUS Widely distributed but little known.



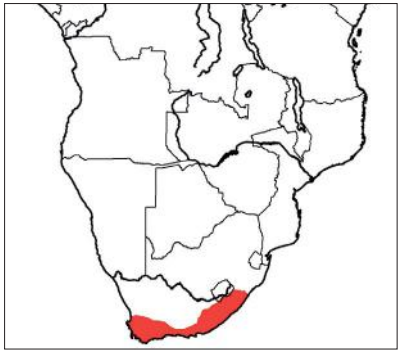
Miombo Genet



Miombo Genet (?) from north Mozambique

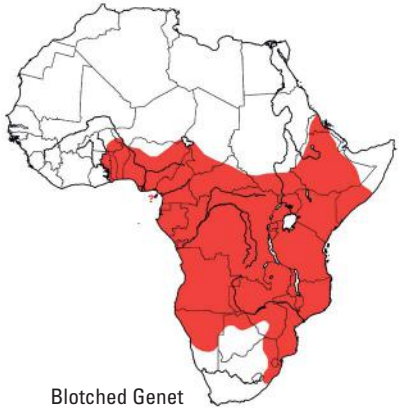
CAPE GENET *Genetta tigrina*

OTHER NAMES Fr. *Genette du Cap*. Ger. *Grossfleck Ginsterkatze*. Swah. *Kanu*.
MEASUREMENTS HB 400–550mm. T 400–540mm. W 1.2–3.1kg.
RECOGNITION A soft-furred, short-legged genet without a well-defined dorsal crest. The ears are broad based and slightly rounded. The tail is soft furred and has a black or smudged tip and some white rings are often incomplete.
HABITAT Both natural Cape vegetation types and cultivated and settled land.
FOOD Opportunistic omnivore. Mainly small mammals and invertebrates with birds mostly during fledging times. Some plant material.
STATUS Not endangered.



Cape Genet

Cape Genet



Blotched Genet

Blotched Genet

BLOTCHED GENET *Genetta maculata*

OTHER NAMES Large-spotted Genet. Fr. *Genette commune à grandes taches*. Ger. *Gemeine Grossfleckgenette*.

MEASUREMENTS HB 400–550mm. T 400–540mm. W 1.5–3.2kg.

RECOGNITION A soft-furred, short-legged genet without a well-defined dorsal crest. The ears are broad-based and slightly rounded. The tail is soft furred, has a black or smudged tip and some white rings are often incomplete. The colours and patterns of the blotchy coat are extremely variable. Furthermore, differently coloured morphs (red or grey-black) co-exist in the same area. This has led to a great proliferation of species and subspecies names.

GEOGRAPHIC VARIATION Recent genetic studies have determined that several taxa formerly regarded as subspecies should be given species status. Of the 20 or so other named subspecies many are currently being revised.

HABITAT Most of sub-Saharan Africa except the Horn of Africa and extreme southern Africa. Rainforest, riverine vegetation, secondary growth, moist woodlands and all moist forest and woodland mosaics. Blotched Genets are well adapted to cultivation and suburbia; also to reedbeds, swamp forest and grassy savannas.

FOOD In comparison with the Common Genet, Blotched Genets take fewer vertebrates, more invertebrates and more fruits. However, both these species rely on rodents as their main staple.

STATUS Not endangered.

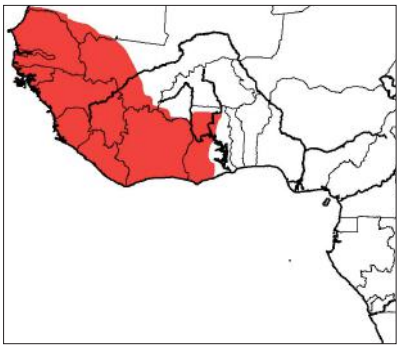
PARDINE GENET *Genetta pardina*

OTHER NAMES West African Genet. Fr. *Genette pardine*. Ger. *Grossfleckgenette*.

MEASUREMENTS HB 410–550mm. T 390–490mm. W 2.5–3.1kg.

RECOGNITION A robust genet with strongly contrasting facial mask. Black mid-dorsal line wide. Spots typically with black outlines around reddish centres but subject to individual variation. Lower limbs sepia and sparingly spotted. Tail has six or seven pale

Pardine Genet

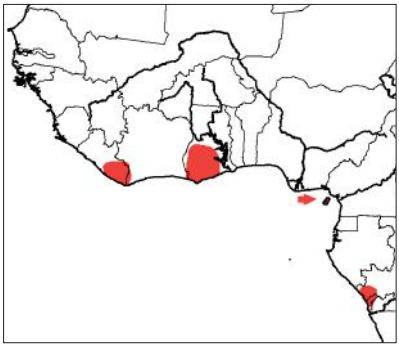


Pardine Genet

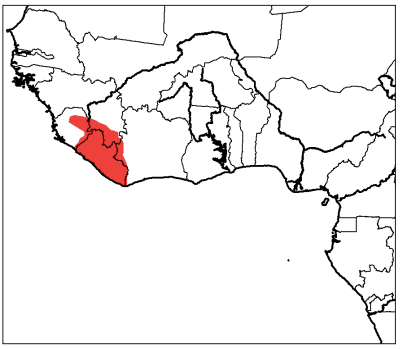
rings, often incomplete, on shortish, mainly black background.
HABITAT Various wooded areas in far western Upper Guinea, possibly west of Volta R.
FOOD Rodents, but frequency of invertebrates has been noted.
STATUS A popular prey for bushmeat hunters, for flesh and ornamental pelt.

KING GENET *Genetta poensis*

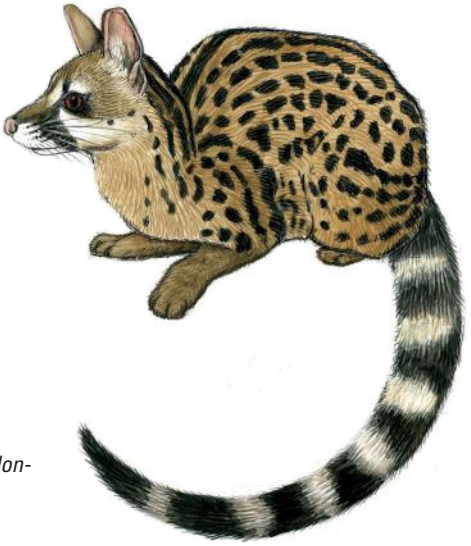
OTHER NAMES Fr. *Genette royale*.
Ger. *Konigs-ginsterkatze*.
MEASUREMENTS HB 350–680mm. T 350–460mm.
W (est. ave.) 2.8kg.
RECOGNITION A large, dark genet of controversial status but erected as a species on genetic criteria. Genetically thought to be of very recent origin, having emerged from a common ancestry with *G. maculata*. Banding of the tail seems to be in the process of being suppressed, with very dark tints on the five or six paler bands. Likewise, blotches tend to amalgamate along the dorsal axis and lower limbs are very dark.
HABITAT Most records are from coastal or near-coastal areas in high rainfall forests between the Congo R. and Liberia.
FOOD Not known, but probably relatively omnivorous.
STATUS Only known from museum skins bought before 1946 and present status remains unknown. Should be considered at risk.



King Genet



Bourlon's Genet



BOURLON'S GENET *Genetta bourloni*

OTHER NAMES Fr. *Genette de Bourlon*. Ger. *Bourlon-genette*.
MEASUREMENTS HB 490–500mm. T 400–420mm. W (est.) 3kg.
RECOGNITION Closely resembling the King Genet, *G. poensis*, but with more discrete spotting and well-marked face pattern. This species also belongs in the *maculata* group and has been erected mainly on genetic grounds. Like *G. poensis*, lighter bands on the tail are muted and less conspicuous than in most genets, implying that tail signals are of less significance for these species.
HABITAT Upper Guinea rainforests.
FOOD Not known.
STATUS Most specimens derive from hunters and bushmeat stalls.

HYAENIDS HYAENIDAE

Striped Hyaena	*Hyaena hyaena*
Brown Hyaena	*Hyaena brunnea*
Spotted Hyaena	*Crocuta crocuta*
Aardwolf	*Proteles cristata*

RECOGNITION Hyaenids are long-legged, long-necked carnivores with large eyes and ears and a blunt muzzle. They have a shaggy, striped or spotted coat and a short, hairy tail. The feet are large, with five heavily padded toes. Shoulders are higher than the hindquarters.
GENEALOGY The earliest hyaenids emerged from a civet-like stock in Eurasia, where they possibly began as an Old World parallel to the earlier emergence of canids in America. In both cases short-legged woodland or forest animals adapted to more open country and to more alert, mobile prey or more dispersed food. Canids have remained the pre-eminent open-country coursers and competition with them probably forced early hyaenids into more specialised niches; their common adaptive strength is sustained trotting or long distance foraging. The first likely fossil hyaenids (still very civet-like) date from about 20 mya. The earliest bone-crushers to appear as fossils are aged at about 10 million years. Of living hyaenas, the Spotted Hyaena represents the relatively small survivor (some were as big as bears) of a diverse, very successful and advanced carnivore/scavenger that ranged from the shores of the Atlantic to those of the northern Pacific. *Crocuta* types emerged earlier but both Spotted and Striped species are recognisable in their modern forms in the fossil record of 7 mya. The Brown Hyaena is an ancient southern isolate but fossil Striped Hyaenas have also lived in southern Africa in the past. Fossil hyaena dung (coprolites) and calcium nodules in some African plains habitats are so numerous as to suggest that a high proportion of *all* mammal bones passed through the hyaena's digestive system in the past.

GEOGRAPHY Once widespread in Eurasia and Africa, hyaenids are now reduced to four rapidly declining species, one of which just survives outside Africa. No species occurs in forest and they are very rare in well-wooded country.

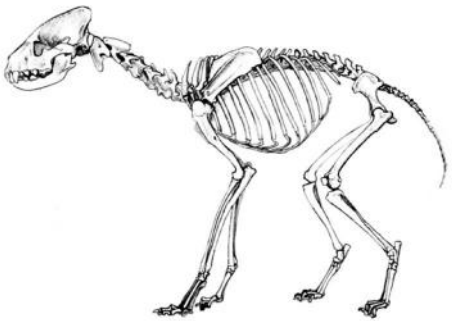
ECOLOGY Hyaenids require a consistent, year-round supply of prey (carrion or, in the case of the Aardwolf, harvester termites) in their relatively open environments. Large anal glands exude two distinct scent marks (one long lasting and the other ephemeral). These serve as long-term territorial 'keep-out' markers or as short-term 'overlap-avoidance' markers.

NATURAL HISTORY Hyaenids have complex social relationships in which use of the home range and contacts with others are regulated by scent signals, loud calls and elaborate behaviour.

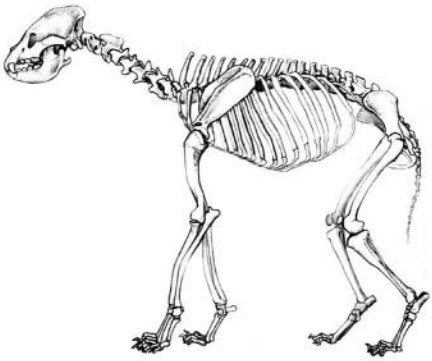
ADAPTATIONS Animals that have long legs also tend to evolve long necks, if only to reach the ground without kneeling. Gaits are strongly influenced by this extension and sloping hindquarters develop mainly because of the need for very tall spinal processes at the shoulder (the main pivot for all gaits, especially the gallop).

It has been suggested that the Aardwolf is a mimic of the Striped Hyaena but differences in size, colour, gait and general demeanour mean that the two species are hard to confuse in the field. Their resemblances are due to the retention of similar features from an ancient common ancestry. Crests are devices for increasing apparent size and are common to many mammals. Striping of the legs may be associated with ritualised fighting and display postures that are common to both species.

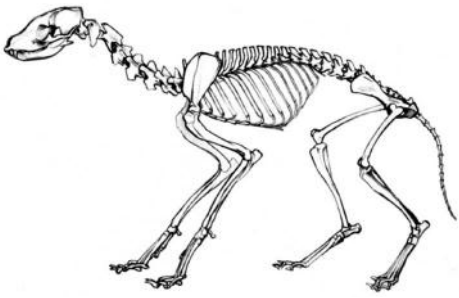
The principal distinctions between hyaenas and Aardwolves are related to their diets, dentitions and digestions. Hyaena skulls are short, deep and wide to accommodate bulky chewing and neck muscles. The carnassial teeth are large in all species but the Spotted Hyaena's are primarily adapted to slice and shear through large bones and thick hides. Carcasses of elephants and other giants would have been a major resource for the much larger Pleistocene Spotted Hyaenas.



Striped Hyaena skeleton.



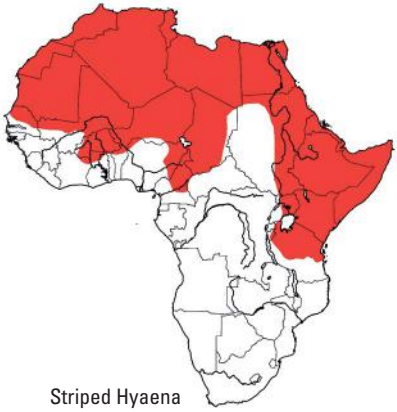
Spotted Hyaena skeleton.



Aardwolf skeleton.

Hyaenids share with civets an unusual digestive physiology and it is possible that an ability to break down complex organic materials, such as bone, chitin and semi-poisonous compounds, was evolved very early on in their common ancestral stock. Today it is the ability to shatter, swallow and digest large mammal bones and teeth (bone is digested in a few hours, teeth take rather longer) that most distinguishes true hyaenas from both Aardwolves and all other carnivores. Hyaenas regurgitate matted hair, bits of horn and other indigestible fragments but, unlike many other carnivores, they never regurgitate meat and always carry cadavers in their jaws. The jaws, neck, shoulders and forelegs are adapted for sustained weight-carrying.

STRIPED HYAENA *Hyaena hyaena*


Striped Hyaena

OTHER NAMES Fr. *Hyène rayée*. Ger. *Streifenhyane*. Swah. *Fisi*.

MEASUREMENTS HB 1.0–1.2m. T 250–350mm. W 25–55kg.

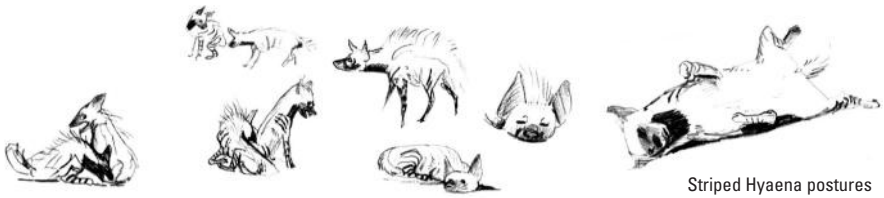
RECOGNITION A tall, slender hyaena with a long, thick neck, pointed ears, large eyes and a blunt black muzzle with a pointed, dog-like nose. The legs and body are striped while the throat is sometimes all black, sometimes densely banded. The fur is long and shaggy, except on the face and lower limbs, and there is a crest that runs from crown to tail. Measurements indicate that an excited hyaena with a raised crest looks 38% larger than a calm hyaena with a flattened-down one!

GEOGRAPHIC VARIATION No subspecies are recognised due to overall variability (there are 22 synonyms for the Striped Hyaena).

DISTRIBUTION Once distributed from Britain to China, but now found only in N and NE Africa, the Middle East, Turkey, the Caucasus, through Uzbekistan to all India, from sea level to 3,000m. The most southerly records are from central Tanzania.

HABITAT Arid steppes and subdesert, *Acacia* scrub and dry savannas, open montane habitats and rocky escarpments. The Striped Hyaena can tolerate high and very cold climates if they are also dry. Home-ranges are very large and individuals leave anal scent-marks on boulders or plants along habitually used paths. They lie up in natural caves or in burrows that are preferably dug by other animals but can be self-dug. Dens are used over extended periods while breeding and subadult animals from a previous litter are known to help feed young siblings. Solitary individuals are less attached to a single den.

FOOD Omnivorous and opportunistic but primarily adapted to coping with bones and carrion. Single hyaenas are known to kill prey up to the size of an adult donkey but they are seldom fast enough to catch alert, free-living animals. Nonetheless, hares, foxes and rodents may be stalked or



Striped Hyaena postures

snapped up. Various well-protected vertebrates, such as tortoises, are easily killed and eaten, and invertebrates, including grasshoppers and termites, are taken. Palm dates, heglig (*Balanites*) and other fruits, including cucurbits (which may be taken primarily for the moisture they contain) are also eaten and, in some areas, scraps from garbage dumps make up the main diet.

BEHAVIOUR Striped Hyaena behaviour differs according to whether or not the Spotted Hyaena is present. Where the two species co-exist the Striped Hyaena is quieter, more retiring and perhaps more solitary and cryptic with regard to dens and raising young. Mature adults of both sexes are intolerant of other members of their own sex. The very protracted dependence of offspring on their mother or parents is partly due to their need to learn foraging routines appropriate to the locality. Adult tolerance declines as the young grow up and appeasement displays therefore become more conspicuous. Averting the head, grimacing, eye-rolling and salivating are all rather dog-like gestures of subordination. A bristling mane, extended neck and nipping lunges are signs of dominance. Meetings between neighbours are accompanied by maximum fluffing out of fur and crests and attempts at mutual intimidation. The anal glands are everted and there are ritualised fights in which the antagonists aim at the sides of each other's thick-skinned necks with 'incisor-nips' made with half-clenched jaws. Such fights, intended to inhibit bone-cracking bites, are often conducted on bent knees, which would appear to keep the slender legs out of harm's way.

All social contacts are abbreviated by the need to forage alone over very large ranges (at least 50km^2 in rich habitats, probably many times larger in poor ones).

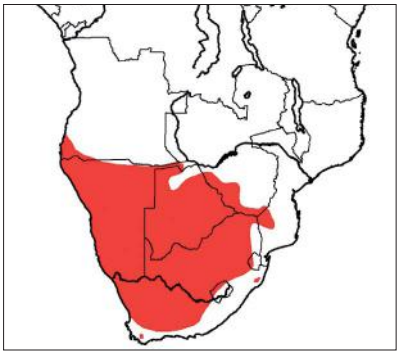
The loudest call is a rarely heard, cackling howl. Staccato whinnies or cackles signify excitement. Threats begin with a growl, rising to a roar and low, snapping lunge. The juvenile want call is a bleat. The adult stress call is more of a moan and hoarse exclamations, 'aah, aah', are uttered when bitten.

ADAPTATIONS The ability of the Striped Hyaena to break up and digest dry bones is undoubtedly its major peculiarity. The skull, teeth and neck bones are appropriately massive. By contrast, the slender body and limbs look weak and flimsy. This sparse frame seems to be built for maximum economy of energy. The Striped Hyaena can trot for long periods at 8km/h, moving for 5–8 hours and covering up to 30km in a night, sometimes with very poor nutritional rewards.

STATUS Once very abundant, especially on the margins of the Sahara desert, the Striped Hyaena has declined over most of its range. It has disappeared from some areas but is still widespread. It is vulnerable to poisoning. Overall, not endangered (IUCN).

BROWN HYAENA *Hyaena brunnea*

OTHER NAMES Fr. *Hyène brune*. Ger. *Braune hyäne*.
MEASUREMENTS HB 1.10–1.25m. T 250–300mm. W 40–55kg.
RECOGNITION This species resembles a dark, heavily caped Striped Hyaena but with a vivid cream-coloured throat, dark brown or slate body and shorter black tail. The pale neck fur forms a distinct mane in healthy adults. The head is like that of the Striped Hyaena but darker.
GEOGRAPHIC VARIATION Five subspecies named but none recognised.
DISTRIBUTION Originally most of Africa south of the R. Cunene and R. Zambezi. Now exterminated over wide areas.



Brown Hyaena

Brown Hyaena

Brown Hyaena with crest and tail hairs erected

HABITAT Currently limited to the Kalahari Desert, the Namibian coastal littoral and less inhabited borderlands in South Africa and Zimbabwe. Formerly the Brown Hyaena ranged throughout the Highveld and most Cape and south-western arid habitats. In spite of its very large territories, the Brown Hyaena uses its range so intensively and leaves anal scent-marks so systematically that it has been calculated that a strange, intruding hyaena will encounter a scent-mark within 250m of entering another 'clan's' territory. In the course of a year the members of a single clan may deposit as many as 145,000 scented tokens of their presence. In addition to anal-gland deposits, the Brown Hyaena tends to leave dung in 'latrines' close to visual landmarks and close to clan boundaries. The deposits not only demarcate land and identify clan members, but progressive deterioration of the odour allows individual foragers to assess how long the deposit has been there, to avoid recently foraged areas and thus to concentrate their energies on less recently foraged areas.

FOOD Primarily carrion, especially during the dry season or when nomadic herds pass through. Surplus food may be hidden nearby or carried back to the den, which may be many kilometres away. The Brown Hyaena also feeds on small mammals, invertebrates and fruits when larger carcasses are not to be found. Beach-combing for dead sea lions, whales and ocean debris is common along the Namibian seashore. Although larger numbers may visit, no more than three hyaenas are commonly seen on one carcass at a time. The Brown Hyaena forages over distances of 1–54km in a night. It is almost entirely nocturnal.

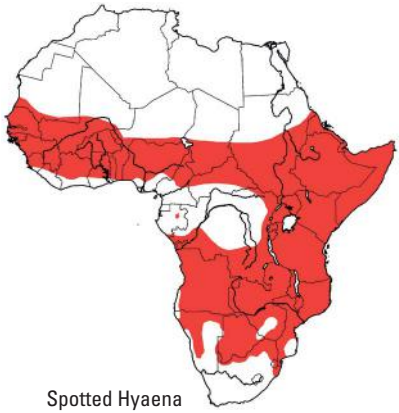
BEHAVIOUR Home-ranges are occupied by a small number of closely related adults (up to three males and five females), their immediate young and some subadults, numbering up to 14 in total. A consistent supply of carcasses encourages slower dispersal. The range varies from about 240 to 480km^2 and is defended against strange hyaenas. Resources tend to be sparsest in the larger ranges. Vocalisations, visual displays and dominance/subordination behaviour closely resemble those of the Striped Hyaena.

Mating is opportunistic; females have a brief oestrus attracting bouts of multiple copulations, sometimes with several males. After a 3-month gestation, up to three young are born blind and deaf. The female secludes herself for the birth and first few months.

ADAPTATIONS Home-ranges are so large and resources commonly so dispersed that single foraging trips may last several days. For lactating females this puts the young at risk and it is common for females to rejoin a central clan den a few months after giving birth. Here lactating females suckle any cub and all ages and sexes bring home food and share it. Young may suck for up to 15 months and do not mature until they are 2½ years old. Communal clan dens may represent the response of solitary foragers to the problems of slow maturation in an environment in which resources are very thinly and widely scattered.

STATUS In spite of being represented in several national parks, the overall range of this species continues to decline. It currently occupies about a half of its original range. The Brown Hyaena is especially susceptible to trapping and poisoning. IUCN rates it as rare and vulnerable.

SPOTTED HYAENA *Crocuta crocuta*



Spotted Hyaena

OTHER NAMES Fr. *Hyène tachetée*. Ger. *Flecken hyäne*. Swah. *Nyangao* (also *Fisi*).

MEASUREMENTS HB 1.0–1.8m. T 250–360mm. W 40–90kg.

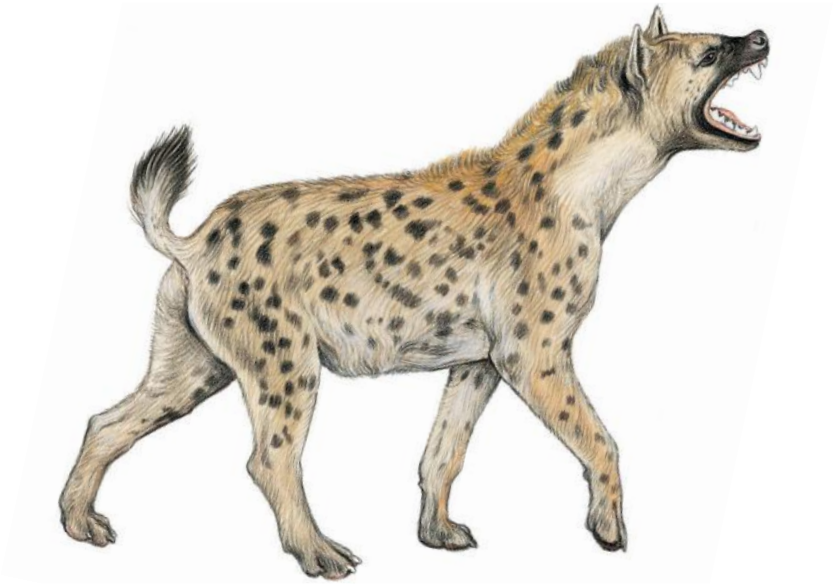
RECOGNITION A powerfully built, dog-like hyaena with a black muzzle and black tip to the short, brushy tail. The body colour may be various tints of brown and slate in young animals but is pale tawny in old animals. Neck, body and legs are splattered with irregular spots and blotches which become fainter with age. Females average 12% heavier than males. The species' best-known peculiarity is 'hermaphroditic' sex organs. The female's clitoris mimics the male penis, can elongate and has a foreskin. Paired swellings in the position of the scrotum consist of non-functional fibrous tissue.

The Spotted Hyaena is more often heard than seen. Its loud, long-distance call, a repetitive and reverberating hoot 'whoo-up', carries for up to 5km (and is most frequently made while walking with the head hanging). Less frequent is its famous 'laugh', a shrill, social-appeasement call that sounds like a maniacal human giggle. Its sloping back and long, thick neck are highly characteristic. A raised tail signifies aggression and the illustration below illustrates a large female (witnessed defending her cub).

GEOGRAPHIC VARIATION Great individual variation invalidates all of nearly 30 synonyms.

DISTRIBUTION Formerly most of non-forested Africa (but always rare in densely wooded country). Although present in North Africa for at least 6 million years, it was not recorded in historic times. Similar early extinctions eliminated *Crocuta* populations across Eurasia. In South Africa the Spotted Hyaena was trapped and poisoned out of settled areas before this century. Active and rapid eradication is currently in progress over large areas of Africa. This renders any distribution map of rather ephemeral value.

HABITAT Open savannas, all *Acacia* communities, montane moors and grasslands, various dry steppes and plains with abundant herbivores are preferred. Although the Spotted Hyaena digs



its own burrows, communal dens are often in caves or crevices in rocky country. Large clans circulate among a few communal dens which are used over many generations (some caves may have been used for centuries). Mounds of excavated and trampled earth, radiating paths and an absence of herbivores modify the immediate surroundings to a den. Very large dens are often surrounded by a scatter of scrapes and shelters that are used by peripheral hyaenas.

FOOD An opportunistic carnivore and scavenger wherever animal remains, from the feeding of other carnivores or humans, or the vicissitudes of nature, is available. The Spotted Hyaena is a scavenger in relation to the amount of carrion available and absorbs a high proportion of it when no easier and fresher alternative is available (e.g. newborn calves during the calving season). Hyaena kills tend to correspond with the vulnerability of prey species rather than their relative abundance. Thus, the fast, well-protected and abundant zebras tend to be under-represented in the hyaena's diet whereas the slower, less common Waterbuck is more frequently killed. Foods taken range from invertebrates, mudfish, reptiles (such as tortoises) to large mammals. Today, household or town garbage is a major resource.

The Spotted Hyaena forages singly (especially in low-density areas) or may live and hunt in groups. Distances covered vary from a kilometre or so to 80km and foraging may take up 1 or 2 hours to a greater part of the night. Some social hunts begin as a group activity, with a direct target, but many build momentum on the initiative of a single hunter. Hunts and kills attract followers, as does the noisy gorging at a carcass. Sometimes an entire clan of more than 50 adults may feed together and, with every animal competing to swallow as much food as fast as possible, the carcass does not take long to demolish. Carrion is frequently cached in bushes, scrapes or under water, but not until hunger is sated, which may involve bolting up to 13kg at a go.

BEHAVIOUR Where food is super-abundant a single clan can number more than 100 (with a range of 35–80 adults). Territories average about 30km^2 in well-stocked wildlife parks but home-ranges are much larger in subdeserts or faunally impoverished areas. Clans build up around a hierarchy of related females and their offspring. Males tend to disperse, females remain. Adult males are essentially peripheral to the clan and only the imperatives of mating (at the height of oestrus) overcomes the male's fear of the larger females.

Up to four cubs are born after a 4-month gestation. In spite of being temporarily blind, the young are precocious and grow fast. Suckled only by their mother, who very seldom carries food, they are sufficiently large to join in at a kill at about 8 months but continue to suckle until they are 18 months old.

The Spotted Hyaena utters begging calls (whines and chatters) and growls or screams in a variety of social situations. Hunting clans tend to socialise intensively in the evening before setting off on a hunt or foraging expedition.

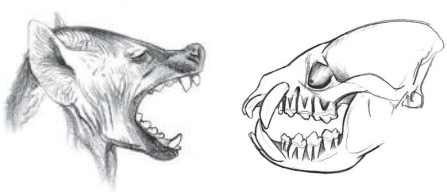
Spotted Hyaena mutual genital inspections and facial expressions

ADAPTATIONS Female mimicry of male genital organs has been found to derive from testosterone levels that are sometimes higher than in the males and begin in the foetus. Testosterone may also fuel their dominant role. Female aggression may ensure that lactating mothers have unimpeded access to all types of food, as well as deterring males from attacking their cubs. Social relations among Spotted Hyaenas centre on avoidance or appeasement of the larger, dominant females. Adult males take the first option but younger males and females, which could scarcely survive outside the clan, appease by lifting a leg and proffering their genitalia for inspection. Although pseudo-penises and scrotums may be by-products of high testosterone levels, they play a part in appeasement or greeting rituals because a display of masculine attributes is a sign of subordination. Unlike other hyaenas, the Spotted Hyaena keeps its anal sacs closed during greetings lest it send a contradictory, aggressive signal.

The primary adaptation of the Spotted Hyaena is its massive teeth, which are able to cut through the bones and skin of all contemporary fauna, including elephants and rhinos. As contemporary

body sizes are smaller than those of many Pleistocene Spotted Hyaenas, its body size has probably declined along with its dietary options (which have become more limited due to the extinction of so many mega-herbivores).

STATUS Decline is accelerating in all areas due to increasing livestock displacing wild communities and the expansion of farming. The Spotted Hyaena is generally regarded as vermin and is readily poisoned. Although still widespread, its long-term future outside wildlife conservation areas is not hopeful.



tooth rooting in Spotted Hyaena skull

AARDWOLF Protelinae

Represented by a single species, the Aardwolf superficially resembles its larger, heavier cousin, the Striped Hyaena, in having slender limbs, a long neck, stripes and a dorsal crest. Like hyaenas, its primary specialisation is in digestion. Instead of detoxifying a diet of decomposing bodies, it is adapted to digesting noxious harvester termites. These surface-feeding, colonial insects are so well protected that few other termite- or ant-eating animals can overcome the barrage of terpene chemicals squirted at them by the soldiers.

The more generalised common ancestors of hyaenas and Aardwolves were likely to have tolerated many toxic and difficult foods (just as civets do today). In the Aardwolf lineage cheek-teeth were reduced to mere pegs while hyaenas developed vice-like, reinforced jaws capable of cracking bones.

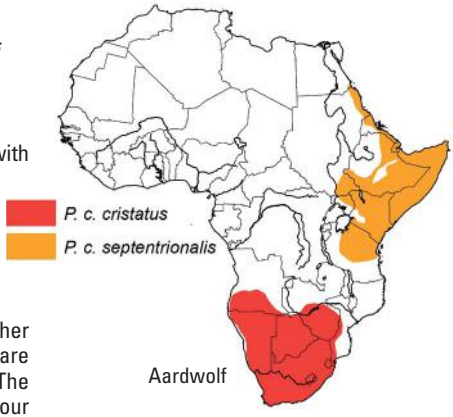
Although the Aardwolf can tolerate a proportion of noxious soldier termites it is adept at rapidly lapping up non-soldiers before they go underground. Walking up to 10km, feeding for about 6 hours, a single Aardwolf is estimated to consume more than a quarter of a million termites in one night.

AARDWOLF *Proteles cristata*

OTHER NAMES Fr. *Protèle*. Ger. *Erdwolf*. Swah. *Fisi ya nkole*.

MEASUREMENTS HB 550–800mm. T 200–300mm. W 8–12kg.

RECOGNITION A slender, cream or tawny animal with narrow, well-spaced stripes and dark brown feet, tail tip and muzzle. A long crest on the neck and back is normally inconspicuous but can stand up and bristle when the animal is alarmed or excited, greatly enlarging its apparent size. The dark skin of the muzzle is without fur and very tough and inflexible, giving the animal a rather fixed expression. Although incisors and canines are well developed, the cheek-teeth are mere pegs. The light creamy fur is often stained with local soil colour from the den.



Aardwolf

The most conspicuous signs of the presence of the Aardwolf are its 'latrines', either uncovered or imperfectly covered by scrapings. Faeces contain termite remains and often include much soil or sand. Scented brown or orange marks are smeared onto bent grass stalks and twigs with the anal glands. These are not conspicuous but are very frequent near 'latrines'.

GEOGRAPHIC VARIATION *P. c. cristatus* (S Africa), *P. c. septentrionalis* (E and NE Africa).

DISTRIBUTION S and NE Africa but absent in intervening Miombo (*Brachystegia*) woodlands.

HABITAT Presence is entirely dependent upon two genera of harvester termites (*Trinervitermes* and *Hodotermes*). These termites flourish best in heavily grazed and trampled grasslands and savannas, especially on sandy plains and plateaus. Although Aardwolves frequently use or modify Aardvark holes or natural shelters, they can dig their own short burrows in sandy soil.

P. c. cristatus

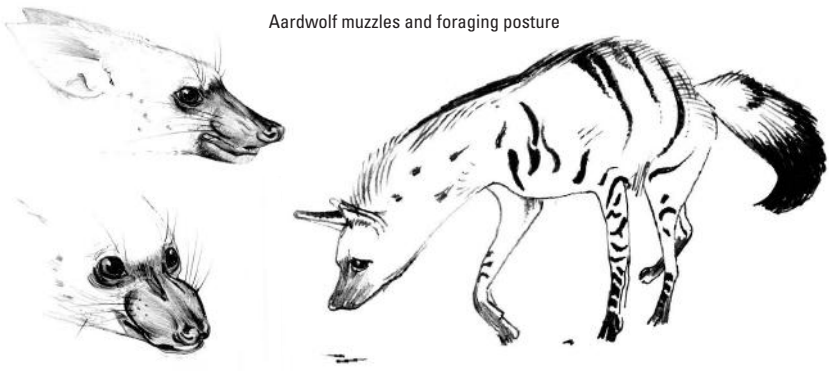
FOOD The availability of the nocturnal *Trinervitermes* and the more diurnal *Hodotermes* may partly determine the times at which Aardwolves are active. In temperate southern Africa the former termite tends to form the summer diet while the latter is favoured in winter. Small numbers of scarab and tok-tockie beetles, grasshoppers, moths and a few small vertebrates are also eaten. Harvester termites forage for dead grass on the surface in small swarms. Aardwolves locate them by listening for the sound of them cutting up leaves and stems. The insects are lapped up and swallowed with minimal chewing, helped down by copious, somewhat glutinous, saliva. All foraging is solitary and follows an eccentric, zigzag course.

BEHAVIOUR Defended territories vary in extent (1–2km^2 in habitats with a high density of termite mounds). In southern Africa a single territory has been calculated to enclose about 3,000 termite mounds (about 165 million termites). Territories are vigorously defended while conditions are good but less so during periods of shortage (when all animals save energy and spend many hours underground). Territories are saturated with anal scent-markings, especially along boundaries, where the holder may paste grass stems every 50m or so. Territorial fights and defensive aggression against jackals (notably near dens in the wet-season breeding period) involve a growling roar and barks, with much chasing and fluffing out of the fur, mane and long dorsal crest. Gestation is variously estimated at 2 and 3 months; young are born in a burrow during the rains. The young, miniatures of the adults, emerge to play above ground at about 6 weeks, at which time they are vulnerable to various medium-sized carnivores. By 4 months they are foraging for termites on their own. A single male and female share a common territory, normally feeding and sleeping apart but both care for the young during their vulnerable period. Both parents may combine to drive off jackals.

ADAPTATIONS Frequently confused with jackals (indeed the Afrikaner name is 'maned jackal'), their overall proportions are those of many generalised but agile small carnivores. Because the very ancient termite-eaters, the Aardvark and pangolins, avoid taking large numbers of harvester termites, it would seem that the Aardwolf became an extreme dietary specialist at a relatively much later date (there are as yet no relevant fossils).

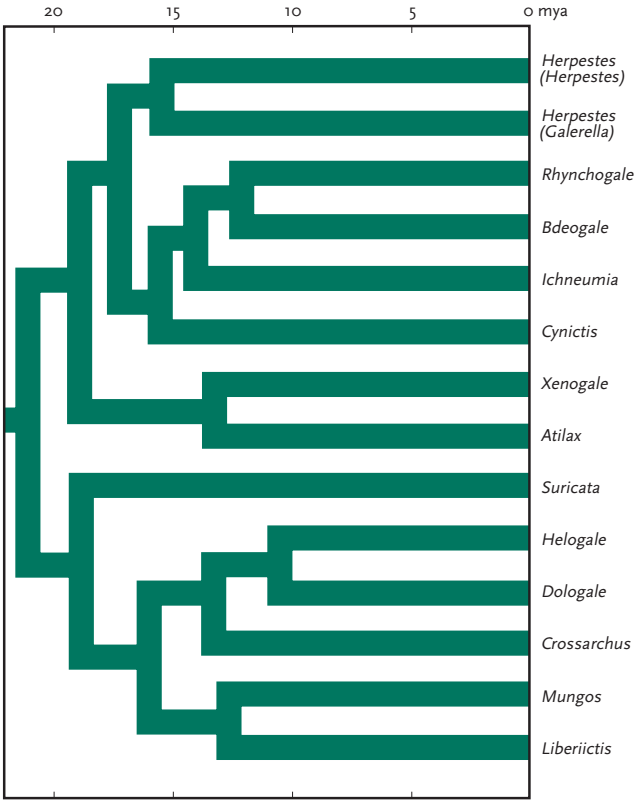
STATUS In spite of nominal protection in most African countries, and recognition of their useful role, Aardwolves are often killed for their furs (eight or more pelts are commonly incorporated in Tswana karosses). Dogs represent the greatest threat to their survival in settled and pastoral areas. Easily dazzled, they are frequent victims of vehicles at night.

Aardwolf muzzles and foraging posture



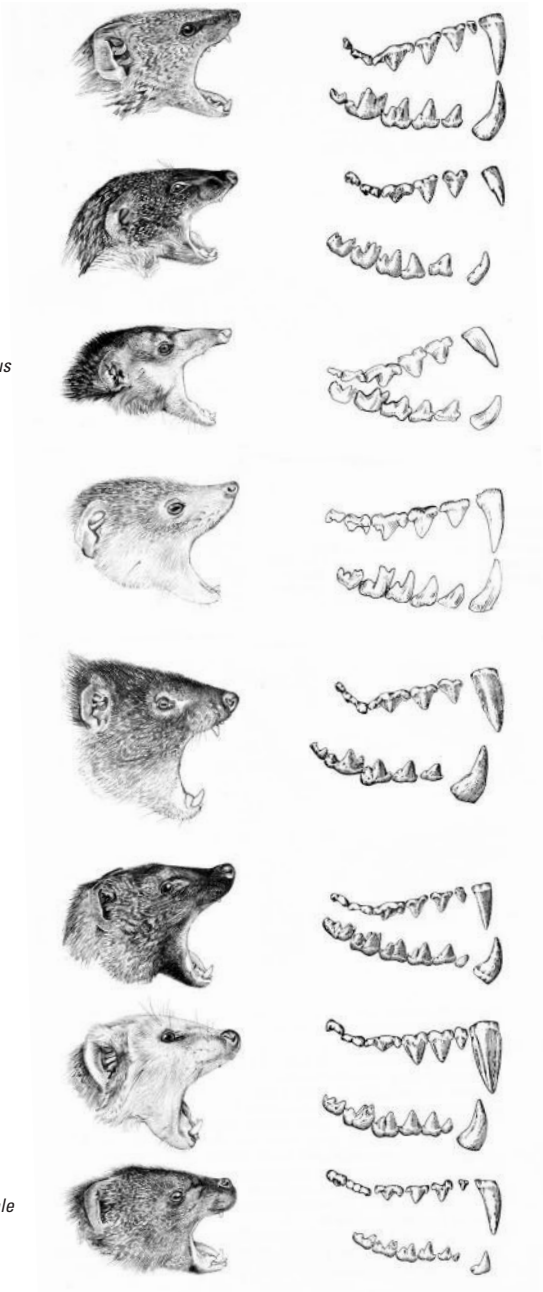
MONGOOSES HERPESTIDAE

Solitary mongooses	Herpestinae
Long-snouted Mongoose	*Xenogale naso*
Marsh Mongoose	*Atilax paludinosus*
Common mongooses	*Herpestes* (5 species)
Yellow Mongoose	*Cynictis penicillata*
Selous's Mongoose	*Paracynictis* (formerly *Cynictis*) *selousi*
White-tailed Mongoose	*Ichneumia albicauda*
Meller's Mongoose	*Rhynchogale melleri*
Four-toed or dog mongooses	*Bdeogale* (4 species)
Social mongooses	Mungotinae
Meerkat	*Suricata suricata*
Banded Mongoose	*Mungos mungo*
Gambian Mongoose	*Mungos gambianus*
Liberian Mongoose	*Liberiictis kuhni*
Cusimanses	*Crossarchus* (4 species)
Savanna Mongoose	*Dologale dybowski*
Somali Dwarf Mongoose	*Helogale hirtula*
Dwarf Mongoose	*Helogale parvula*



Tentative phylogenetic tree for African Herpestidae (after Patou *et al.* 2009).

Small to medium-sized carnivores with a long body and tail and shortish legs. Primarily terrestrial, mongooses have coarse, grizzled coats (never blotched or spotted). A few have striped rumps. All have inconspicuous ears, small eyes and a more or less pointed muzzle. They have complex anal sacs that differ structurally from the perineal civetone glands of viverrids. Some have cheek-glands. Teeth, numbering 34–40, are distinctive for each genus (see below).



Herpestes $\frac{3.1.4.2}{3.1.(3–4).2} = 38–40$

Mungos $\frac{3.1.3.2}{3.1.3.2} = 36$

Crossarchus $\frac{3.1.3.2}{3.1.3.2} = 36$

Helogale $\frac{3.1.3.2}{3.1.3.2} = 36$

Atilax $\frac{3.1.3.2}{3.1.3.2} = 36$

Ichneumia $\frac{3.1.4.2}{3.1.4.2} = 40$

Bdeogale $\frac{3.1.4.2}{3.1.4.2} = 40$

Rhynchogale $\frac{3.1.4.2}{3.1.4.2} = 40$

An ancestral mongoose entered Africa more than 20 mya and then bifurcated into two major lineages, one the 'solitary mongooses', Herpestinae, the other 'social mongooses', Mungotinae. A convenient model or prototype from which all mongoose tooth-rows can be derived is provided by the genus *Herpestes*. The dentition and gapes of eight genera are shown opposite. Solitary mongooses embrace both dentally conservative (*Herpestes*, *Ichneumia*) and more derived, specialist species (*Atilax*, *Rhynchogale*, *Bdeogale*).

The evolution and biogeography of social mongooses is discussed later.

All species are ground-dwelling predators of invertebrates and small vertebrates but some include fruits or other vegetable matter in their diets. Although some are able to do without water (presumably extracting it from prey), most species are water-dependent inhabitants of forests, woodlands, savannas and marshes. Many species adapt to changed conditions or resources by enlarging their range, intensifying activity or by diversifying their diet.

A majority of species are solitary and many of these are nocturnal. A few form pairs for variable lengths of time. At least 11 species are social (and mostly diurnal) – discussed later.

All mongooses depend on scent to communicate and to mark territories. It is likely that anal secretions constitute long-lasting, individual signatures, while cheek-gland secretions produce a short-term, status-related signal that can easily trigger immediate aggression. Cheek-glands appear never to be rubbed without the accompanying anal signature, a precaution that may protect known individuals from attack while heightening aggression against unattractive aliens.

The ability of several species to roll and crash-crack eggs and to kill dangerous snakes is well known. Both are instances of the manipulative skills, speed and versatility of mongooses in their hunting techniques.

The radiation of mongooses in Africa has involved numerous and subtle specialisations in diet and niche that are expressed particularly in their differently shaped noses, ears, jaws, muzzles and whiskers.

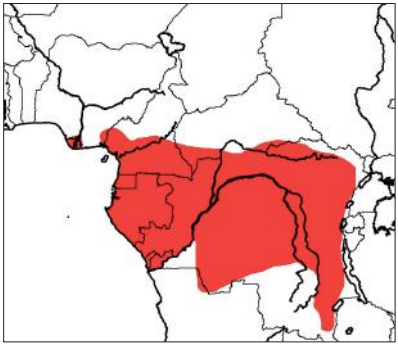
SOLITARY MONGOOSES Herpestinae

Embracing eight genera and 15 species, the individual adaptations of solitary mongooses are discussed under species profiles. *Herpestes* includes two highly successful and wide-ranging species (*H. ichneumon*, *H. sanguineus*) and at least three locally adapted species (*H. pulverulentus*, *H. flavescens*, *H. ochraceus*), each with very restricted ranges. A majority of Herpestinae occupy eastern and southern Africa, however, the biogeographic line that separates the south–east realm from the centre–west realm has divided *Bdeogale* such that one species (*B. nigripes*) inhabits equatorial centre–west forests while all other species occupy the south–east.

LONG-SNOUTED MONGOOSE

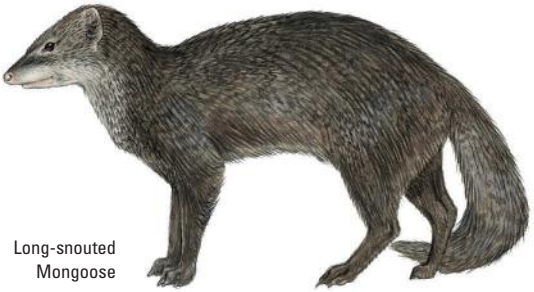
Xenogale naso

OTHER NAMES Long-nosed Mongoose.
Fr. *Mangouste à long museau*.
Ger. *Langnasenichneumon*. Swah. *Bongobo*.
MEASUREMENTS HB 520–590mm. T 360–430mm. W 3.0–4.2kg.
RECOGNITION A large, mainly diurnal, dark, shaggy mongoose with relatively long legs, a thick tail and pointed muzzle. The head is slightly paler than the deep sepia-black grizzled body and tail. The pale, sparsely haired mouth region is well demarcated from the dark, almost black upper muzzle.
HABITAT Main forest block from the western Rift Valley to the Niger delta, where they live close to clear forest streams. They are clumsily semi-arboreal. Extensive monitoring of bushmeat stalls has shown that this species is commoner and has a wider distribution than was previously thought. Escalation of the bushmeat trade in all rainforest countries could mean the Long-snouted Mongoose becomes extinct, certainly rare, before even being adequately studied.



Long-snouted Mongoose

FOOD Omnivorous; recent studies on diet suggest arthropods. Unusually, shrews are a significant part of their vertebrate diet, as are rodents. They are known to eat snails (a rare prey for carnivores), fruits are also eaten, and they are reputed to take carrion.
STATUS Rare. Not listed by IUCN.

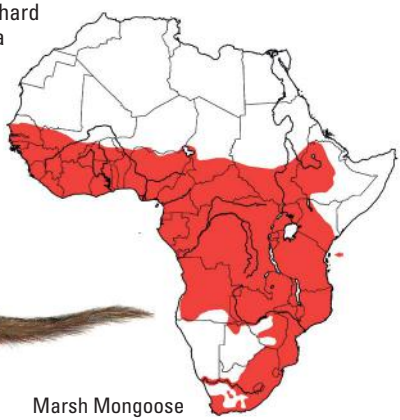

Long-snouted Mongoose

MARSH MONGOOSE

Atilax paludinosus

OTHER NAMES Fr. *Mangouste des marais*. Ger. *Sumfichneumon*. Swah. *Nguchiro wa maji*.
MEASUREMENTS HB 440–640mm. T 310–410mm. W 2.0–5.0kg.
RECOGNITION Large, dark-brown mongoose with thick, shaggy fur on the neck, body and tail but short, sleek fur on the fingered hands and feet. The hands have soft, naked palms and sensitive, flexible fingers. The blunt, slightly upturned muzzle is distinctive and the entire tooth-row is well developed and powerful.
GEOGRAPHIC VARIATION 16 subspecies have been described. Three regional types, with ill-defined borders, have been proposed. These are: *A. p. paludinosus* (South Africa): brown–black. *A. p. pluto* (W Africa): black. *A. p. robustus* (E Africa): grizzled mahogany.
DISTRIBUTION All well-watered regions of sub-Saharan Africa. Absent from the Somali and Namib–Kalahari arid and semi-arid regions. Marsh Mongooses range from sea level up to about 2,500m.
HABITAT Marsh Mongooses inhabit river courses and lakeshore areas in otherwise inhospitable regions. They are more generally distributed in forested or humid areas and are one of a small community of animals living in papyrus swamps. Shelter is required for breeding and may be excavated in termitaries. Alternatively, the burrows of Aardvarks or other animals may be used (in more extensive marshes a floating nest may be constructed in a dense reed thicket).
FOOD Freshwater crabs, snails, mussels, frogs, lungfish (*Protopterus*) and catfish (*Clarias*); insect larvae, reptiles, small mammals, birds and their eggs, fruits.
BEHAVIOUR Marsh Mongooses are territorial and forage individually or in pairs with young. During droughts territories appear to be used more intensively and activity (which is predominantly nocturnal) may continue well into the day. Both latrines and scent deposits are used to mark territories and regulate social contacts. Loud bark-growls are uttered as a threat against intruding mongooses or dogs. Moans and purrs (contact?) and bleats (excitement) are also uttered on occasion. Little is known about the reproductive behaviour of this shy and retiring species. However, up to three smaller animals often accompany one or sometimes two adults.
ADAPTATIONS Marsh Mongooses use their long, sensitive fingers to find food in turbid water or soft mud. They take their weight on their hindlegs while rapidly sifting back and forth through the water. Large or hard prey, such as crabs and mussels, is broken against a rock by hurling it down from a standing position.
STATUS Widespread and common. IUCN status: least concern.

Marsh Mongoose



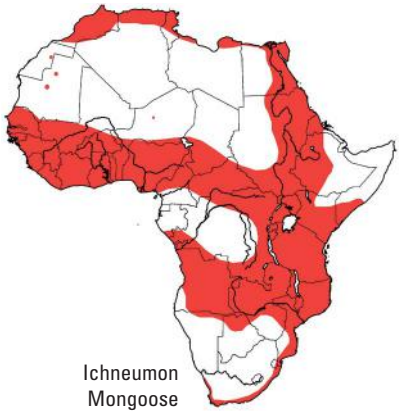
COMMON MONGOOSES *Herpestes*

Ichneumon Mongoose	*Herpestes ichneumon*
Slender Mongoose	*Herpestes sanguineus*
Angola Slender Mongoose	*Herpestes flavescens*
Small Grey Mongoose	*Herpestes pulverulenta*
Somali Slender Mongoose	*Herpestes ochraceus*

ICHNEUMON MONGOOSE

Herpestes ichneumon

OTHER NAMES Egyptian Mongoose. Fr. *Mangouste ichneumon*. Ger. *Ichneumon*. Swah. *Nguchiro*.
MEASUREMENTS HB 450–600mm. T 330–540mm. W 2.2–4.1kg.
RECOGNITION A long-bodied, low-slung mongoose with a slender, almost snake-like head. The long, markedly tapered tail ends in a conspicuous black tassel. In most postures the legs are largely concealed by long fur, increasing its reptile-like form. The grizzled coat varies in shade or tint.
GEOGRAPHIC VARIATION 25 subspecies have been described but there is so much variation between individuals and regions that a thorough revision of subspecies is needed.



Ichneumon Mongoose

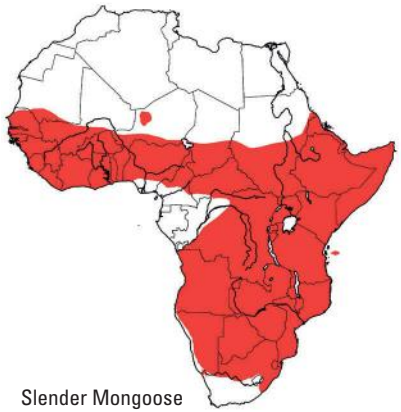
DISTRIBUTION Africa, S Spain and Israel. Very widely distributed in Africa but absent from the Sahara, Horn of Africa, Namib Desert and other waterless regions; also absent from true forest.
HABITAT Commonest in flat, grassy areas on floodplains, coastal littorals, lakeshores and broad river valleys; also on rolling moist savannas and in extensive forest clearings where grass has become dominant. It appears to be a speedy colonist of disturbed or seasonally flooded areas. It is water-dependent and a good swimmer.
FOOD Rodents, reptiles, frogs, birds and various invertebrates. The broad range of prey is matched by the animal's exceptional ingenuity and versatility in hunting and catching techniques (most ending in a fast, snapping lunge). Subterranean food items (larvae, crabs, eggs, and insects) are rapidly dug out with well-clawed forepaws.
BEHAVIOUR While this mongoose is normally seen singly or in small family parties, larger

associations may form around two or more females, their immediate young and some previous young. Larger groups, seldom seen in Africa, may be a response to high population densities supported by abundant resources and an absence of competition from other carnivores. These enlarged female units are associated with a single male, which drives male offspring away and only joins the females sporadically. After a 2-month gestation up to four young are born, blind and helpless, in a den or thicket. Blind until 3 weeks and taking their first solid food at 1 month, they are self-sufficient by 4 months. Some become wholly independent only after 1 year. This prolonged immaturity is linked with exceptional playfulness and much exploratory behaviour which helps to turn up more food of a wide variety. Females normally produce only one litter per year but rich resources may encourage both biannual breeding and more social behaviour, with older offspring helping to feed and care for their younger siblings. This mongoose has a wide vocabulary of chatters (excitement), hoots and clucks (contact), spits, screams and growls (threat and defence).
ADAPTATIONS '*Ichneumon*', from the Greek word for 'tracker', describes this mongoose's most conspicuous characteristic, which is to be seen trotting along with its head down. This is thought to be scent-tracking along well-established trails (laid by the mongoose itself or by other members of its family). Recent observations have revealed that a single family or group of families share a well-known home-range and a single anal-scent beacon, consisting of a stone, soil or plants. All family members frequently mark this beacon by rubbing their glands all over it. In the process their long fringe of abdominal hair becomes impregnated with scent (this probably being its primary function). Deviations from regular trail-tracking are mostly carried out in pursuit of food and are followed by a return to the nearest trail point to resume 'tracking'. The snake-like appearance of the Ichneumon Mongoose, enhanced by its fringe, sometimes results in the animal being mobbed by birds. With its lightning strike it may then be able to catch birds that would otherwise be impossible to hunt.
STATUS Very widespread but commonest in areas with few other mongoose species. Strong scenting of trails may make them vulnerable to dogs. IUCN status: least concern.

SLENDER MONGOOSE

Herpestes sanguineus

OTHER NAMES Fr. *Mangouste rouge*. Ger. *Rotichneumon*. Swah. *Lukwiru*.
MEASUREMENTS HB 260–340mm. T 230–310mm. W 350–800g.
RECOGNITION Long-bodied, short-legged, partly arboreal mongooses, extremely variable in colour. The digits of the hands and feet splay readily and are armed with small but sharp, hooked claws. The tip of the tail is usually black-tipped. Young have olive-green eyes up to 6 months, reddish amber thereafter.
GEOGRAPHIC VARIATION Great variation is evident among 70 named subspecies. Among them are *ochracea* and *flavescens*, which are now generally accepted as distinct species.
DISTRIBUTION South of Sahara and Aïr massif to Orange R., from sea level up to 2,500m.



Slender Mongoose

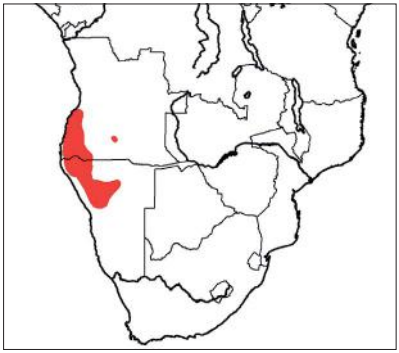
HABITAT All wooded, savanna, thicket and forest habitats (including the driest *Acacia* and the wettest forests); also occurs in extensive papyrus and forest swamps. Slender Mongooses use termitaries, hollow and creviced trees, burrows and holes for shelter.
FOOD Rodents, insects, reptiles, frogs, birds (including nestlings and eggs). Insect larvae (notably blowfly larvae at carcasses) have been frequently recorded. Slender Mongooses are mainly diurnal foragers, with a characteristic gliding, horizontal gait punctuated by pauses in which they stand up, periscope-like, to scan the environment.
BEHAVIOUR Both sexes hold exclusive territories of variable size. Adult males may tolerate smaller males but confrontations within and between sexes are common. Loose associations between pairs are long-lasting. Marking posts are inconspicuous and may be close to sleeping places. Latrine sites are used but ostentatious marking appears rare.

Up to three young are born after just under 2 months' gestation. The blind and helpless young open their eyes at 3 weeks and begin eating solid foods at 4 weeks. They can become independent at 10 weeks but may stay longer with the mother if she has no second litter. Two litters a year are common. Slender Mongooses utter a faint purr (contentment), a soft hiss (playful), a bird-like whistle or hoot (contact) and a harsh, scolding caterwaul (alarm/aggression).
ADAPTATIONS Slender Mongooses resemble squirrels in their ability to climb trees at speed. This greatly increases their ability to reach certain resources and may explain their abundance and widespread distribution.
STATUS Not endangered. However, *H. s. swalius* is rare and localised. IUCN status: least concern.

ANGOLA SLENDER MONGOOSE

Herpestes flavescens

OTHER NAMES Kaokoveld Slender Mongoose. Fr. *Kaokoveld mangouste rouge*. Ger. *Kaokoveld rotichneumon*.
MEASUREMENTS HB 310–350mm. T 320–360mm. W 550–907g.
RECOGNITION A slim, strongly grizzled yellowish-brown, mahogany or black mongoose with a long, black-tipped tail. Face and feet are darker. The skull is intermediate between *H. sanguineus* and *H. pulverulentus*.
HABITAT Inhabits the coastal plain in Angola and northern Namibia. Even within this limited range it has been recorded only from rocky areas or their immediate vicinity. Where it is sympatric with *H. sanguineus*, the latter prefers the more wooded areas, *flavescens* the more arid, stony country.
FOOD Mainly rodents (notably the rock-crevice-dwelling Noki *Petromus*), birds, reptiles and invertebrates (insects made up the greater part of an analysis of 126 scats).
STATUS Not endangered.



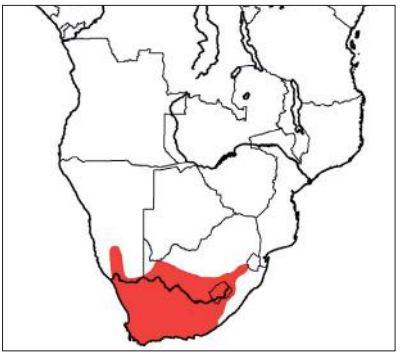
Angola Slender Mongoose

SMALL GREY MONGOOSE

Herpestes pulverulenta

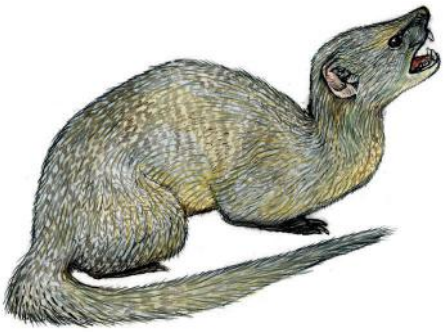
OTHER NAMES Cape Grey Mongoose. Fr. *Mangouste grise du Cap*. Ger. *Kleinichneumon*.
MEASUREMENTS HB 280–370mm. T 230–360mm. W 370–800g.
RECOGNITION A rather uniformly grizzled, grey mongoose with a thickly furred tail (without a black tip). Face and feet are slightly darker and very finely vermiculated. It is seen singly, in twos, or in small family groups.

Small Grey Mongoose



Small Grey Mongoose

HABITAT Mainly overgrown bushy country in all habitat types south of the Orange R. (where it replaces the Slender Mongoose). It prefers dry rocky ground and hillsides and is particularly common on the coastal plain.
FOOD Mainly invertebrates (insects, crabs, larvae, earthworms, snails) and shellfish in estuaries; also rodents, reptiles and birds.
STATUS Not endangered.



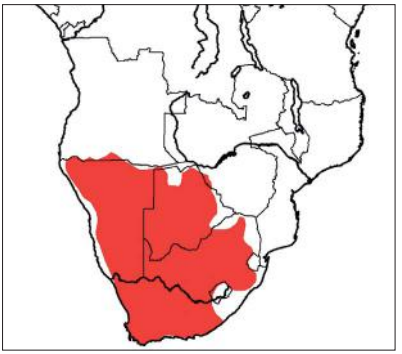
Somali Slender Mongoose

SOMALI SLENDER MONGOOSE *Herpestes ochraceus*

OTHER NAMES Fr. *Mangouste de Somalie*. Ger. *Somali manguste*.
MEASUREMENTS HB 220–290mm. T 220–270mm. W (est.) 400–700g.
RECOGNITION A grizzled, grey, brown or russet mongoose with a well-furred, tapered tail (without black tip). Muzzle and feet slightly darker than body colouring.
HABITAT Notably hilly country in all habitat types of the Somali arid region.
FOOD Probably small vertebrates and invertebrates.
STATUS Not known.

YELLOW MONGOOSE *Cynictis penicillata*

OTHER NAMES Fr. *Mangouste fauve*.
Ger. *Fuchsmanguste*.
MEASUREMENTS HB 250–400mm. T 180–300mm. W 440–800g.
RECOGNITION A small, alert mongoose with dainty, rather weak-looking limbs and a sharply tapered face, with forward-facing eyes over a short muzzle. The tail is bushy, usually with a tapered white tip.



Yellow Mongoose

Yellow Mongoose

In the southern part of its range it is very yellow, whereas in the north it is grey. The coat is dense and woolly and usually conceals the long, lithe form of the body. Animals frequently sunbathe for an hour or more in the early morning, especially in winter.

DISTRIBUTION S Africa, Karoo, Cape and Kalahari to S Angola.

HABITAT Favours open sandy areas, often valley bottoms, pans or clearings within more heavily overgrown or wooded country. The warren complexes are often of great age and their slight elevation may be the result of sustained excavation over long periods. Often shared with ground squirrels and Meerkats (which also dig), warrens can have more than 80 entrance holes.

FOOD Invertebrates, especially beetles, their larvae and harvester termites. Food preferences vary with locality and from season to season so that rodents or other vertebrates may be important in certain areas. Fruits may be taken *in extremis*. Concerted attacks on snakes may culminate in feeding but have the character of attack against a potential predator because most foods are found and dispatched by individual foragers.

BEHAVIOUR Markedly hierarchical packs numbering up to 50 animals are dominated by a breeding pair. Social structure is diffuse in that the lowest-ranking members are forced to spend most of their time away from the pack or on its margins. Such 'hangers on' are often elderly or infirm animals. Up to five young are born in the burrow between October and March. They join their older siblings for their first excursions at 2 months and are adult-sized by 10 months. As with other social mongooses, the dominant female provides the reproductive continuity in a pack and all members help to raise her young. However, it is the dominant male who is the central beacon and it is his activity and individual scent that defines the pack's identity. The most energetic individual in the pack, he marks the boundaries of the territory and the body of every pack member. He is also the principal digger of holes.

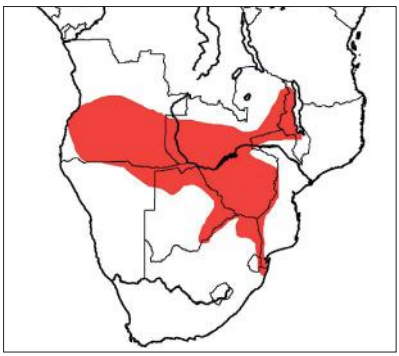
STATUS Widespread and common. IUCN status: least concern.

SELOUS'S MONGOOSE *Paracynictis* (formerly *Cynictis*) *selousi*

OTHER NAMES Fr. *Mangouste de Selous*. Ger. *Trugmanguste*.

MEASUREMENTS HB 350–480mm. T 280–430mm. W 1.3–2.2kg.

RECOGNITION A delicate-looking, long-bodied, long-legged mongoose with a bushy, white-tipped tail and a grizzled grey coat with dense underfur that shows through to give ochre tints (especially



Selous's Mongoose

on the flanks, thighs and chest). The ears are widely spaced, rounded and fairly prominent. The feet are dark brown, have four toes and longish hard nails. It is almost wholly nocturnal.

DISTRIBUTION Upper Zambezi basin and peripheral uplands of the northern Kalahari basin with extensions towards Malawi and Swaziland. Although it lives mainly in regions of summer rainfall (with periodic frosts from May to August), it appears to be absent from the coldest South African uplands, as well as from the surrounding warmer lowlands.

HABITAT Areas of open, short grass; well-drained, sandy country with open Mopane (*Colophospermum*) scrub, Baikiaea teak woodland and fire-climax miombo (*Brachystegia*) woodland with open floors. It is also found on cultivated land and ranches. It frequently makes use of ready-made burrows in harder soils but generally digs its own two-tiered labyrinths in the loose, well-drained, sandy soils of the region.

FOOD Invertebrates, with a strong preference for beetles and their larvae, termites and grasshoppers. Numerous other species are taken opportunistically. Mice, reptiles and frogs are commonly eaten; birds only rarely. Most foods are found by smell and excavated from shallow retreats. Selous's Mongoose often visits cattle pens to dig for dung-beetle larvae.

BEHAVIOUR Life histories are likely to revolve around burrows, which are dug slowly and laboriously but which retain lasting importance as key landmarks and refuges. As many as four animals have been taken from a burrow but these were thought to be a family. Animals are normally seen singly out in the open. Most births occur during the rainy season (August–March). Litters of up to four young have been recorded.

ADAPTATIONS The slender, long-legged build of Selous's Mongoose suggests that rapid digging ability is of less importance than speedy escape. An abundance of bolt-holes is provided by numerous other burrowing animals that favour the same sandy habitat (notably Aardvarks, porcupines and springhares, as well as various other carnivores). Probably a relict species of generalised habits, this mongoose may overcome competitive exclusion by other herpestids (such as the White-tailed Mongoose) as a result of its unique strategy of rapid flight above ground and ready refuge underground.

STATUS Widely distributed and favoured by current pastoral economy. It is vulnerable to dogs. Not endangered.

WHITE-TAILED MONGOOSE

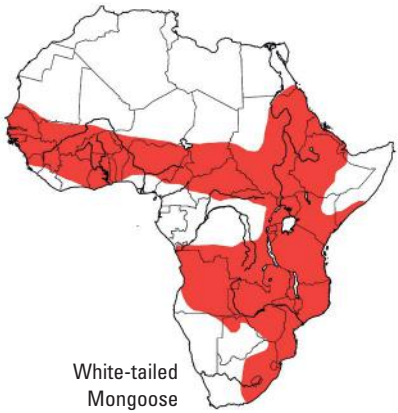
Ichneumia albicauda

OTHER NAMES *Mangouste à queue blanche*. Ger. *Weisschwanzichneumon*. Swah. *Karambago*.

MEASUREMENTS HB 470–710mm. T 350–500mm. W 2.0–5.2kg.

RECOGNITION A slender, long-legged mongoose, delicate and somewhat fox-like, with a thick, silver-tinted coat. It usually has a white tail but coat coloration is very variable. Unlike the dog mongooses (which have four toes), this species has five toes. Very dark morphs with black tails are common in Uganda. It is normally wholly nocturnal.

GEOGRAPHIC VARIATION 12 subspecies have been named but individual variation obscures regional groupings.



White-tailed Mongoose

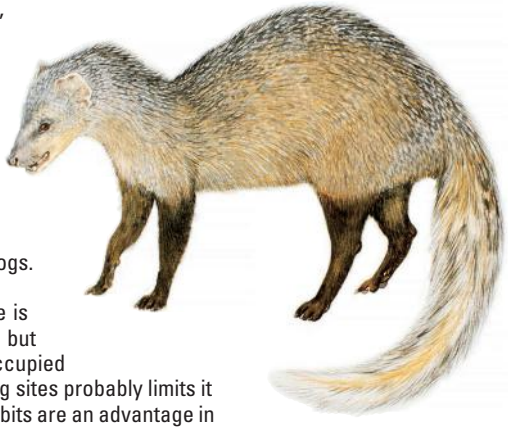
DISTRIBUTION Widespread in sub-Saharan Africa except for the rainforests and the south- west. In spite of being common in the Somali arid zone it is totally absent from equivalent habitats in the Kalahari and Namibia.

HABITAT This very versatile mongoose flourishes in grassy savannas, tropical woodlands, grassy clearings in former forest areas, cultivation, suburbia and ranchlands.

FOOD Mainly invertebrates, with termites, beetles and their larvae being the preferred foods. Mice, frogs and reptiles are also taken very frequently, but fruits very infrequently.

BEHAVIOUR Although normally solitary, adult females are known to share home-ranges amicably with adult offspring and as many as nine individuals have been seen foraging together. Localised food and delayed dispersal may explain these temporary aggregations. Home-ranges are probably

only a few hectares in the richest habitats, but are estimated at up to 8km^2 on the plains of Kenya (on the Serengeti Plains they range from 40 to 123ha). Animals have been seen to scent-mark the boundaries of their ranges and to repel unwelcome intruders with raised, fluffed-out tails and ritualised postures and displays. They utter a loud, fox-like bark and scream very loudly when fighting or attacked by dogs. Up to four young are born in a burrow.



White-tailed Mongoose

ADAPTATIONS The White-tailed Mongoose is a good long-distance walker and trotter but a poor digger. Its dependence on unoccupied burrows or easily modified natural denning sites probably limits it severely in some areas. Its generalised habits are an advantage in unstable ecological conditions but exclude it from areas with large and diverse carnivore populations, where dietary specialists can out-compete it (this may explain its absence in SW Africa).

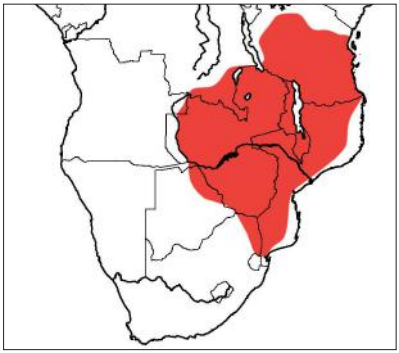
STATUS Prone to rapid fluctuations in numbers. Not endangered. IUCN status: least concern.

MELLER'S MONGOOSE

Rhynchogale melleri

OTHER NAMES Fr. *Mangouste de Meller*. Ger. *Maushund*.

MEASUREMENTS HB 440–500mm. T 280–400mm. W 1.7–3.1kg.



Meller's Mongoose

RECOGNITION A dark, muddy-coloured mongoose with long legs and tail, shaggy, coarsely grizzled fur and a blunt, broad and rather retroussé nose. Meller's Mongoose has a somewhat domed forehead and a wide, swollen upper lip, well furred and without a slit up the midline. The tail can be black, white or with lighter underfur beneath black guard hairs. The toes are arranged symmetrically in pairs (fifth toes are vestigial). A distinctive feature is the prominent 'reverse cow-licks' of long fur on each side of the throat. Where these meet the cheek fur there is something of a ruff. The rounded ears are partially concealed by long fur on the temples and forehead.

DISTRIBUTION Rarely seen; supposedly patchily distributed over a wide area of SE Africa from sea level to 1,850m.

HABITAT Moist areas with thick grass and abundant termitaries, particularly in wide, shallow and well-watered valleys. Meller's Mongoose appears to require dense cover throughout the year

and most records are from the eastern, moister region of miombo (*Brachystegia*) woodlands. It is rarely seen in areas where fires are extensive and frequent.

FOOD Termites, particularly harvester termites (*Hodotermes*) and the larger *Macrotermes*. Meller's Mongoose also takes termite-eating snakes and centipedes, and grasshoppers, beetles and frogs have also been recorded. Fallen fruits may be locally or seasonally important. Termites can only be taken in small numbers at a time because this mongoose is not a digger. The combination of a specialised diet and the need to avoid exposure would seem to confine Meller's Mongoose to a rather narrow feeding niche.

BEHAVIOUR Solitary and little-known, this extremely shy and reclusive animal is apparently rather silent, hollow sinuses on the forehead may act as resonators, in which case long-distance contact calls could be of special significance. Up to three young are born in a burrow or rock crevice.

ADAPTATIONS Blunt, broad lips and shaggy fur may be minor adaptations to a termite diet in this species but the blunt teeth suggest a softer, less carnivorous diet than other mongooses. The digestive physiology of Meller's Mongoose has not been studied but must be moderately specialised in order to cope with a termite diet (the peculiar cow-lick on the throat may allow biting soldier termites to be scratched away more easily). These minor modifications to the generalised mongoose frame suggest late and marginal adaptation to a niche that is dominated by the Aardvark, pangolins, Aardwolf and Bat-eared Fox in drier, more exposed habitats.

STATUS Very poorly known. Habitat change and exposure to domestic or feral dogs are possible dangers. Indeterminate.

FOUR-TOED OR DOG MONGOOSES *Bdeogale*

Bushy-tailed Mongoose	*Bdeogale crassicauda*
Sokoke Dog Mongoose	*Bdeogale omnivora*
Black-legged Mongoose	*Bdeogale nigripes*
Jackson's Mongoose	*Bdeogale jacksoni*

RECOGNITION Long-bodied, long-tailed, moderately tall mongooses with rounded ears, a blunt muzzle and very symmetrical four-toed feet. They have a dense, woolly fur and guard hairs of variable length and colour. All have black or dark-brown limbs. The bare rhinarium around the nostrils is broad and rounded. There is a shallow groove down the midline of the upper lip. All species have peculiarly straight upper canines with bladed ridges fore and aft. They generally move slowly and deliberately but can lope along at a trot when not foraging and can run fast when chased. They may be active during the day as well as at night, especially during the wet season.

GENEALOGY Most closely related to Meller's Mongoose, species in this group include the less specialised Bushy-tailed Mongoose, which lives in drier forests and woodlands, and the more specialised, ant-eating Black-legged Mongoose, which lives in equatorial moist rainforests. Like other mongooses, no species has entirely abandoned omnivory (perhaps because they remain marginal specialists compared to pangolins and sengis).

Their four symmetrical toes have lost versatility in digging and handling food but the more compact feet are better suited to walking and trotting.

GEOGRAPHY Like Meller's Mongoose, dog mongooses appear to originate in the drier forests and woodlands of East Africa where they are associated with valley bottoms and soft soils.

ECOLOGY In strongly seasonal environments moisture and dense vegetation last longest in valleys. Dog mongooses appear to be more restricted to such valleys in the dry season. In spite of being very common in their preferred habitat, alert, fast-moving animals, such as frogs and birds, are not typical prey. They are very quiet and careful foragers with a preference for larger prey that is vulnerable to a slow, stealthy approach, such as grazing rodents, inactive but larger invertebrates (e.g. caterpillars or spiders), or very small fauna that are both surface-dwellers and abundant (e.g. ants and termites).

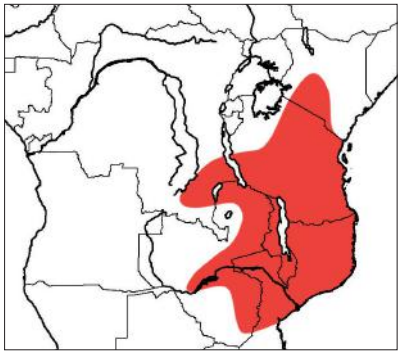
NATURAL HISTORY Dog mongooses are seldom seen, due to their extreme caution and the dense, difficult vegetation they favour. They are solitary, although temporary family groups may form. Evidence from Crowned Hawk-eagle kills suggests that the Bushy-tailed Mongoose may be commoner (and more diurnal) in Tanzanian forest areas than is generally supposed. This may be true of other species.

ADAPTATIONS The blunt, rounded molars of these species are similar to those of Meller's Mongoose and imply good ability to grind soft foods and little cutting or slicing ability on tougher, harder items.

The dog mongooses have a less restricted diet than Meller's Mongoose but are likely to need an extensive year-round range because resources are gathered along a rather narrow, linear habitat and their food, while common, tends to come in small helpings.

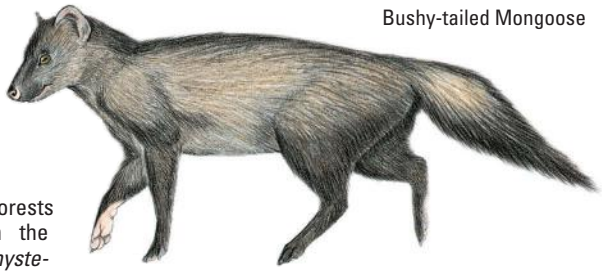
BUSHY-TAILED MONGOOSE

Bdeogale crassicauda



Bushy-tailed Mongoose

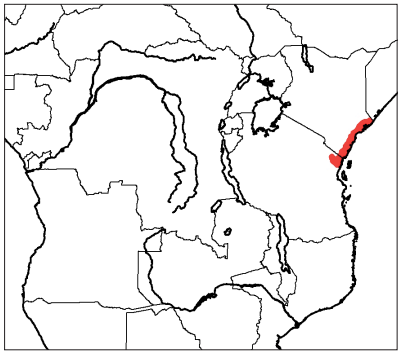
OTHER NAMES Fr. *Mangouste à queue touffue*. Ger. *Buschschwanzichneumon*. Swah. *Kitu*.
MEASUREMENTS HB 400–500mm. T 200–300mm. W 1.3–2.1kg.
RECOGNITION A brown or black mongoose with a bushy, tapered tail, relatively prominent ears and a blunt dog-like muzzle. The teeth are the least rounded, with the sharpest cusps of any *Bdeogale* species. Colouring varies locally but is relatively uniform, with long black guard hairs over a paler, dense underfur. Limbs are black or deep brown.
GEOGRAPHIC VARIATION *B. c. crassicauda* (SE Africa), *B. c. puisa* (E Tanzania and N Mozambique), *B. c. tenuis* (Zanzibar), *B. c. nigrescens* (Kenya highlands). Note: *puisa* and *nigrescens* are provisional.



HABITAT Coastal thickets, dry forests and well-vegetated valleys in the moister eastern miombo (*Brachystegia*) woodlands; also dense vegetation around rocky outcrops and escarpments. Distribution is fairly continuous along the coast, but more patchy inland.
FOOD Ants and termites; also caterpillars, crickets, grasshoppers, beetles, their larvae and other invertebrates, mostly picked off the ground or vegetation. Snakes and lizards, burrowing toads and rodents are more rarely eaten. Very active prey appears to confuse Bushy-tailed Mongooses but more acquiescent prey is dealt with deliberately by means of deep, forceful bites.
STATUS Widely distributed but nowhere common. They are eaten in some areas and vulnerable to dogs. Not endangered.

SOKOKE DOG MONGOOSE

Bdeogale omnivora



Sokoke Dog Mongoose

OTHER NAMES Sokoke Bushy-tailed Mongoose. Fr. *Mangouste de Sokoke*. Ger. *Sokokeichneumon*. Swah. *Kitu (ya) Sokoke*.
MEASUREMENTS HB 340–450mm. T 180–240mm. W (est.) 0.7–1.6kg.
RECOGNITION A small mongoose with a pale cream-coloured body and dark-brown limbs and tail. There are longer, black-tipped guard hairs in the tail, on the rump and more sparsely on the back. Head and shoulders are palest, almost white. Teeth are distinctive (oval and very wide with an enlarged last molar). This species is predominantly nocturnal.
HABITAT Only known with certainty from coastal forests between the R. Galana and Mombasa. However, it could possibly occur as far north as the R. Juba in Somalia. The lowlands immediately below the Usambara Mts are inhabited by

Sokoke Dog Mongoose

dog-mongoose upper tooth rows

Bushy-tailed Mongoose

Sokoke Dog Mongoose

Black-legged Mongoose

the Bushy-tailed Mongoose. If supposed sightings of the Sokoke Mongoose in the Usambara Mts are confirmed there should be a sharp altitude boundary between the two forms. The Sokoke forest consists of very old miombo (*Brachystegia*) woodland growing on white marine sands. The animals shelter in small riverine patches of evergreen thicket but forage more widely. They range through a mosaic of forest, savanna and cultivation.

FOOD The first specimens collected contained insects, birds and fruits (hence the name *Bdeogale omnivora*).

STATUS Only 4,332ha of Sokoke forest are nominally protected (illegal pit-sawing continues there). Cleared forest can even revert to sterile sand in this area. Hunting with dogs is widespread. Highly endangered with extinction. A captive breeding programme has been suggested.

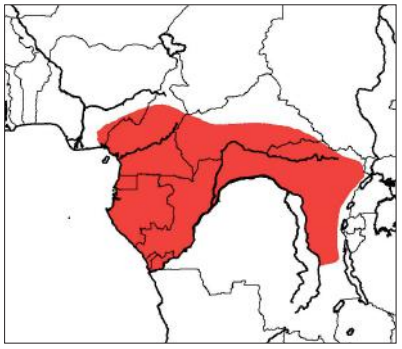
BLACK-LEGGED MONGOOSE

Bdeogale nigripes

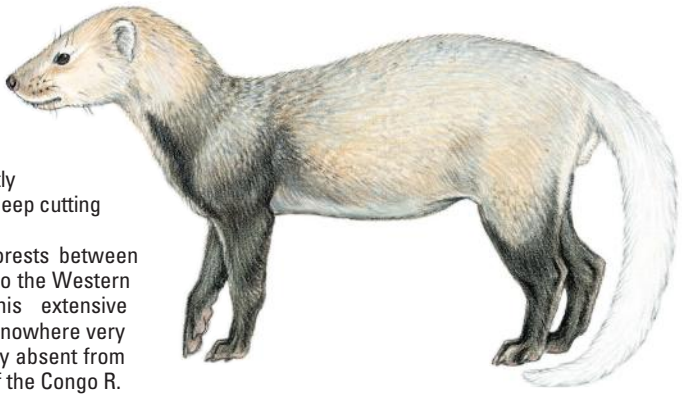
OTHER NAMES Fr. *Mangouste à pattes noires*. Ger. *Schwarzfuss ichneumon.*

MEASUREMENTS HB 550–650mm. T 350–400mm. W (est.) 2.0–3.5kg.

RECOGNITION A large, pale mongoose with black limbs and a white tail (face and rump are also white in some individuals). The tail is long but only moderately bushy. Fur on the body is dense and thick but relatively short. Shoulders may be grey or show an upward extension of the black or sepia forelimb colour. Molars are small and rounded while the upper canines are particularly straight and long, with sharp-bladed ridges fore and aft. Although the precise function of the canines is not known, they are evidently capable of delivering a deep cutting stab.



Black-legged Mongoose



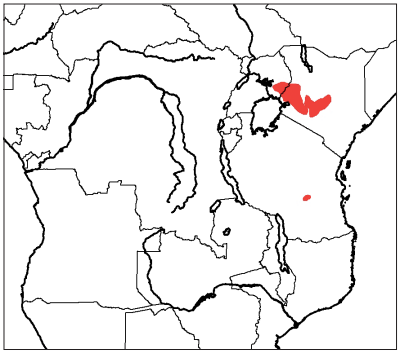
HABITAT Lowland rainforests between the Cross R. in Nigeria to the Western Rift Valley. Within this extensive range it is localised but nowhere very common. It is apparently absent from low-lying areas south of the Congo R.

FOOD Mainly ants, notably army ants (*Dorylus* and *Myrmecaria*), and other insects; also a variety of invertebrates, including snails and crabs. Vertebrates, including rodents and frogs, have been recorded. Fallen fruits are taken occasionally.
STATUS Widely distributed but poorly known. Not endangered.

JACKSON'S MONGOOSE

Bdeogale jacksoni

OTHER NAMES Fr. *Mangouste de Jackson*. Ger. *Jackson ichneumon*. Swah. *Ngogo*.
MEASUREMENTS HB 520–570mm. T 270–360mm. W 2–3kg.
RECOGNITION Often regarded as a montane isolate of the Black-legged Mongoose, this species is distinguished by its much longer fur, especially on the tail, and very yellowish tints on the neck and throat. Young but breeding animals may be well below average adult size. It is a mainly nocturnal and crepuscular species.
HABITAT Montane forests and bamboo zones on East African mountains; also recorded from lowland forest immediately south of Mt Elgon.



Jackson's Mongoose

FOOD Analysis of about 40 boluses revealed that 40% (by volume) of the adult diet consists of insects, mostly army ants of the genus *Anona*; remains of caterpillars, beetles, millipedes, snails, lizards and snake eggs were also found. About 80% of the juvenile's diet is rodents (compared with over 5% in adults), with the rest mostly lizards, beetles and birds. Coping with well-defended columns of army ants may therefore depend on maturity and learning, which suggests that adaptation to this diet is relatively recent. This is also likely to apply to other *Bdeogale* species.
STATUS The very limited range and low density of this rare species suggests that it is very vulnerable. Some of its range is in currently well-protected areas.

SOCIAL MONGOOSES Mungotinae

At an early stage in their evolution, some mongoose populations became more social. This branch has remained distinct ever since. Other than living in places with both predators and abundant bolt-holes, sociality in mongooses has no obvious explanation but several observers have demonstrated that social living has, indeed, evolved in response to selection by predators, especially raptors and snakes. Both open and some forested habitats support significant guilds of both predator types. Attrition in social mongooses is offset by producing large numbers of young and expending much energy in caring for the young and being super-vigilant. Alarm calls, flight, even 'rescues' and coordinated responses to predators are common. Genetically, Meerkats (*Suricatta*) derive from the earliest beginnings of social living in mongooses. Here, among such

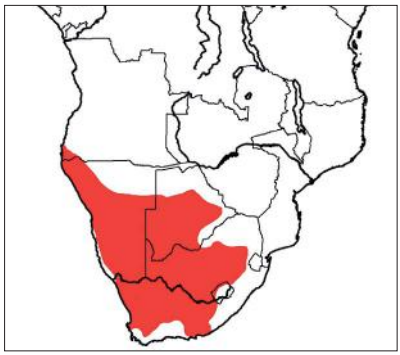
non-forest species there is a strong correlation between social living and demonstrable exposure to relentless predation. The widespread Banded Mongoose *Mungos mungo* and apparently relictual Liberian Mongoose *Liberiictis kuhni* are later branches but contemporary genetics reveal that their common ancestor also gave rise to smaller species. Their descendants split along the classic centre–west/south–east divide: cusimanses (*Crossarchus*) became forest animals while the ancestors of dwarf mongooses *Helogale* occupied the south–east. What drove this phylogenetic decline in size?

The common dwarf ancestor can be predicted to have been a single very wide-ranging species. It is likely that a relict offshoot of that early ancestor survives in the rare central African Savanna Mongoose *Dologale dybowskii*. Intermediate between *Crossarchus* and *Helogale* in size and general morphology, this species also bridges both regions geographically and ecologically. The few observations of this species suggest a close association with termitaries, which is relevant to the fact that its close relative *Helogale parvula*, the species with the greatest exposure to predators, is the smallest. There are special ecological and behavioural reasons for this. Even more than other social mongooses, *H. parvula* is assailed by very many predators. Furthermore, their dispersal through the landscape correlates closely with a high density of termitaries. A major constraint on size is probably the mongooses' need to fit or flit down narrow termitary ventilation chimneys (serving as ubiquitous bolt-holes as well as social dens). Termites thus provided essential but highly structured refuges from the raptors and mammalian carnivores that otherwise would have exterminated the mongooses. The pre-existence of other animals and the ecological impact of their behaviours is a topic that deserves more attention in evolutionary biology.

The vulnerability of small mongooses to predation may be one factor encouraging communal living. Periodic food bonanzas may be another. If the frequency of litters increases as well as the overall population density the rate of dispersal through the young is also slowed. This forces young from previous litters to become helpers in their parental family. The development of dominance hierarchies and social subordination also seems to facilitate mongoose sociality.

MEERKAT *Suricata suricata*

OTHER NAMES Suricate. Fr. *Suricate*. Ger. *Scharrtier*.
MEASUREMENTS HB 245–310mm. T 190–240mm. W 620–970g.
RECOGNITION An ochre-grey mongoose with a rotund body, muscular, well-clawed forearms, a round head and a tubular muzzle. The tail is thinly haired, tapered and shorter than the body. The eyes are surrounded by 'masks' of black skin and fur, thrown into strong contrast by white brows and cheeks. The large snout-nose is also black and conspicuous. The upperparts are well furred and the rump is banded with about eight stripes. By contrast, the greyish skin of the abdomen shows through the sparse white fur of the underside. The pale underside is prominently displayed when the animal stands upright on its hindlegs. In order to help regulate its body temperature the Meerkat often sprawls on its belly on damp ground or warm rocks, stands up with belly forwards, or lolls on its back in the early morning sun.
GEOGRAPHIC VARIATION *S. s. suricata* (South Africa and Kalahari), *S. s. marjoriae* (Namib Desert).
DISTRIBUTION South Africa, Namib Desert and Botswana in the Kalahari, Karoo and Highveld, in open, periodically cold upland country.
HABITAT Kalahari *Acacia* bush, Karoo scrub and Highveld rangelands. Meerkats favour dry, open, often stony, country with short or sparse woody



Meerkat

growth, mainly short grasses and extensive open pans or 'vloere'. They are commonest in rangeland grazed by large herds of wild or domestic stock. Their warrens are most frequently dug in hard, compacted soil close to water-holes or pans in areas of high ungulate concentrations. Five or six warrens, sometimes of very long standing, form clusters in favoured areas and may be shared with other mammals, notably ground squirrels, which also extend them. Clusters of burrows lie within the territory of a single territorial Meerkat pack which rotates its tenancy. Warrens vary in size and extent, the largest having up to 90 entry holes, the smallest fewer than 10. They may have up to three depth levels, with the deepest 3m below the surface. Meerkats almost always stay within easy reach of a warren or bolt-hole. All nights, and part of the coldest winter days and hottest summer days, are spent in their shelter.

FOOD Mainly insects associated with grassland and large herbivore herds: harvester termites, larvae and pupae of dung beetles, flies, butterflies and moths. Insect-predators, such as spiders and scorpions, are taken incidentally, as are mice and reptiles. Foraging is individual but carried out in close formation. Meerkats are very thorough and different foraging patches are visited every day. When food resources in the vicinity of a warren have been exhausted, the pack decamps to another warren. In this way an irregular circuit of warrens is maintained. In dry weather tsamma melons, succulents, tubers or fruits may be chewed, probably for the moisture they contain.

BEHAVIOUR Packs hold territories of 200–1,000ha. Packs average about 10 (up to 30) animals and may include several breeding pairs. Adults may squabble over food but early studies saw little aggression. More intensive observation has revealed that both males and females have hierarchies, and expulsions (especially among females) force subordinates out. Males may occasionally change packs (seldom without conflict). Males are the principal markers of territories, using anal glands, and all pack members fiercely threaten and attack trespassing neighbours.

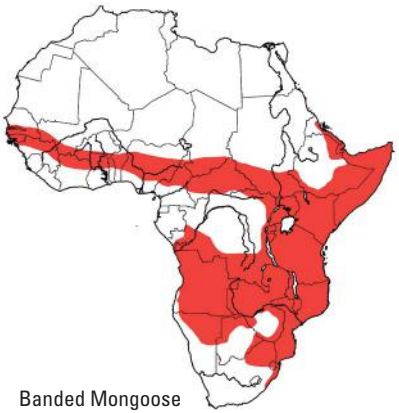
Up to five young are born, after an 11-week gestation, in a grass-lined chamber in the warren. A single dominant female can birth four litters in a year. Breeding can be continuous but most births occur in the warmer, wetter months (October–April). Young become relatively independent at 10 weeks and reach adult size by about 6 months. The main contact call is a soft murmur, infants chirp and trill and juveniles utter a high-pitched begging call. Scolding clucks or cheeps signify alarm, as does a sharp bark. A growling bark is uttered in threat.

ADAPTATIONS Living in very exposed and relatively cool habitats, Meerkats avoid predators (mainly birds of prey) by staying close to their warrens and being highly alert. Smaller terrestrial predators are threatened en masse by all animals fluffing up their coats, snapping and spitting at once. The animals also all jump up and down, giving the illusion of advance. Sunbathing, group-nesting and retreat into warrens are all strategies to help maintain viable body temperatures. Captives have lived more than 20 years but maximum life-spans in the wild are probably about 15 years.

STATUS Extirpation of wild herbivores, spread of cultivation, rabies control, dogs and their diseases have caused local declines but periodic famines or rain failures are main precipitators of serious die-offs. Nonetheless, numbers recover fast due to their exceptional fecundity. Overall, not endangered. IUCN status: least concern.

BANDED MONGOOSE *Mungos mungo*

OTHER NAMES Fr. *Mangue rayée*. Ger. *Zebramanguste*. Swah. *Nkuchiro*.
MEASUREMENTS HB 300–450mm. T 150–300mm. W 1.5–2.25kg.
RECOGNITION A chunky, coarse-haired mongoose with short, muscular, well-clawed legs. It has a prominently banded rump, grizzled upperparts, darker limbs and muzzle, and a pale, thinly haired underside. Colour and size vary such that animals are large and dark in moist habitats and small and pale in drier habitats. It is strictly diurnal.



Banded Mongoose

GEOGRAPHIC VARIATION 20 subspecies have been described but these are in need of revision. Four distinctive regional types can be distinguished: *M. m. mungo* (W Africa), *M. m. zebra* (Horn of Africa), *M. m. taenianotus* (South Africa), *M. m. colonus* (E Africa).

DISTRIBUTION Woodlands, savannas and grasslands of East and central Africa. Also in a broad belt between the Sahara desert and rainforests (where they have been successful colonists of cultivation and large-scale clearances).

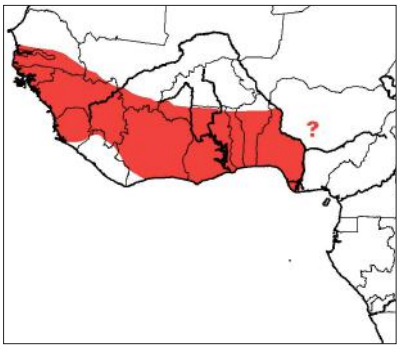
HABITAT Various habitats, ranging from forest/cultivation mosaics to arid *Acacia* scrub and open, short grasslands. They are closely associated with termitaries (which are readily modified into burrows or warrens).

FOOD Termites and beetle larvae (especially in rangelands); cryptic litter fauna in more forested areas, supplemented by small vertebrates. Banded Mongooses forage in a loose formation, maintaining contact by frequent chirps, twitters or churrs.

BEHAVIOUR Banded Mongooses live in packs that can reach about 40 members before dividing into smaller groups with an average of between 15 and 20 members. Packs range over exclusive territories of up to 130ha where up to 40 dens and burrows are resources worth fighting for. Neighbouring groups compete most fiercely for refuge termitaries close to their shared boundaries. Packs typically include three or four breeding females and a dominant male. Hierarchies are based more on age, size and individual assertiveness than on sex. Pack membership is stable but young males may emigrate and splits are normal when numbers increase. The obvious risks of inbreeding are offset by both males and females visiting neighbouring packs in search of copulations. When newborn young are in a den, lactating females other than their mothers may suckle them. Pack members are reluctant to leave the warren en masse so that foraging trips by subgroups tend to be short. Up to four young are born after a 9-week gestation. Females frequently synchronise birthing, but only *within* a pack. Adults will play with young. Pups join the pack foraging by 5 weeks. Mortality is very high.

ADAPTATIONS Anal-gland scent-marking is very frequent, especially among high-ranking males. Landmarks in the territory (stones, stumps, termitaries, etc.) are marked daily. Every member of the group is also marked, mainly on the rump. When presented to another mongoose, the striped area elicits a strong marking response, especially during periods of excitement (e.g. encounters, arrivals, departures and forays into open land where all members are exposed). All pack members therefore share a strong communal odour. Marking is most intense when the writhing pack of snapping, snarling animals is threatening a medium-sized to small predator. Entire packs are known to rush and rescue a pack member seized by a predator.

STATUS Not endangered. IUCN status: least concern.



Gambian Mongoose

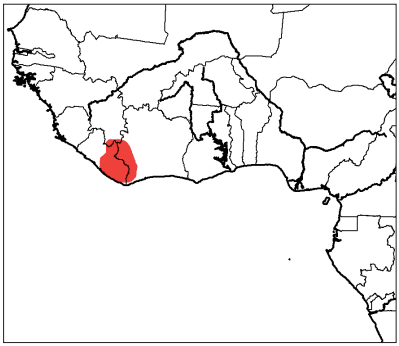
GAMBIAN MONGOOSE

Mungos gambianus

OTHER NAMES Fr. *Mangue de Gambie*. Ger. *Gambiamanguste*.
MEASUREMENTS HB (est.) 330–360mm. T (est.) 180–220mm. W (est.) 1–2kg.
RECOGNITION A compact, coarse-haired mongoose with plain grey upperparts, ochraceous underparts and dark outer surfaces to the limbs. The white chest is separated from the grey nape by a bold black stripe on the side of the neck. The tail is bushy and tapered. The forefeet are well clawed.
HABITAT Moist savannas, forest/cultivation mosaics, grasslands and woodlands from Senegal to the R. Niger. This diurnal colonial species lives in packs of up to 25 animals.
FOOD Invertebrates with some vertebrates. This mongoose twitters continuously while foraging in long grass.
STATUS Little known, but apparently widespread and common.

LIBERIAN MONGOOSE *Liberiictis kuhni*

OTHER NAMES Fr. *Mangue du Liberia*. Ger. *Liberia-kusimanse*.
MEASUREMENTS HB 400–450mm. T (est.) 180–220mm. W 2.0–2.3kg.
RECOGNITION A long-clawed, long-nosed, forest mongoose with a thick dark coat and bushy tail. The very undershot mouth parts, chin and chest are off-white. There is a prominent black stripe on the neckside. This species has very reduced cheek-teeth but long, sharp canines and is reputed to put on a fierce display when trapped.
HABITAT Currently known only from the upper reaches of the Cess R. valley in Liberia and Taï NP in Côte d'Ivoire. Its present range (probably much reduced) is thought to be bounded by the valleys of the R. St John and R. Sassandra. It is known only from low-lying areas and stream banks in overgrown, old secondary forest and in deciduous rainforest growing on sandy soils. Lack of earthworms may be the main factor excluding it from areas with hard lateritic soils.



Liberian Mongoose

FOOD Earthworms and insect larvae are found in streambeds and sump areas by energetic digging with the claws, followed by sniffing and grubbing with the snout. Entire areas of soft soil can be ploughed up in this manner, possibly by family parties. This mongoose is also reputed to dig larvae out of dead palm trunks and it is a competent climber.
STATUS Named in 1958, the first live specimen was caught and photographed in 1989. Rare and localised, this species is seriously threatened with extinction by forest clearance and intensive and uncontrolled hunting for bushmeat. IUCN lists as threatened.

CUSIMANSES *Crossarchus*

Ansorge's Cusimanse	*Crossarchus ansorgei*
Common Cusimanse	*Crossarchus obscurus*
Cameroon Cusimanse	*Crossarchus platycephalus*
Alexander's Cusimanse	*Crossarchus alexandri*

Dark, shaggy mongooses with a snout-like nose and a tubular muzzle. The claws of the forefeet are very well developed. The face and limbs have very short, tight fur but the body appears to be fat due to a dense underfur overlain by darker guard hairs.

Cusimanses have radiated into four distinct regional species. The most generalised of these, Ansorge's Cusimanse, bears some resemblance to the Gambian Mongoose. It occupies drier forest types in the south of the Congo R. basin and has a short, blunt muzzle. The species with the longest muzzle is Alexander's Cusimanse, which also inhabits the Congo basin but is commonest north of the river, where *C. ansorgei* is absent.

Strictly equatorial and, for the most part, lowland rainforest species, they are specialists in feeding on the cryptic fauna of the forest floor and in rotting logs, both on invertebrates and vertebrates. Beetle larvae, snails and earthworms are prominent in the diets of several species. Fruits and mushrooms are only eaten by some species.

Cusimanses are diurnal mongooses that form family parties numbering up to 20 animals. Their sociality probably originated in non-forest ancestors but cooperative behaviour proved effective in surviving similar pressure from forest floor predators. Both sexes perform frequent anal-marking (the male particularly so before mating). Up to four young are born after a 10-week gestation and reach maturity at 9 months. Captive specimens have bred three times a year.

Long guard hairs over a warm and relatively waterproof undercoat suggest adaptation to frequent drenchings. The short-furred extremities are also well suited to a muddy existence and slimy foods in that they are easily rubbed or licked clean. Home-bases are unlikely to play as important a role in the survival of cusimanses as they do in the case of non-forest, social mongooses (except during the breeding season, when the blind, helpless young must be secure). As yet there are no indications of attachment to burrows, nor have elaborate warrens been recorded. They commonly shelter under or in fallen logs or in dense tangles of lianas. Packs appear to be 'campers' that keep moving in regular circuits over their territory.

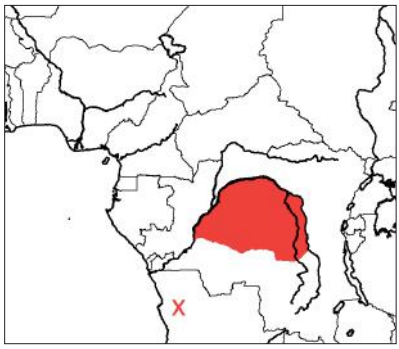
Ansorge's Cusimanse

Common Cusimanse

Alexander's Cusimanse

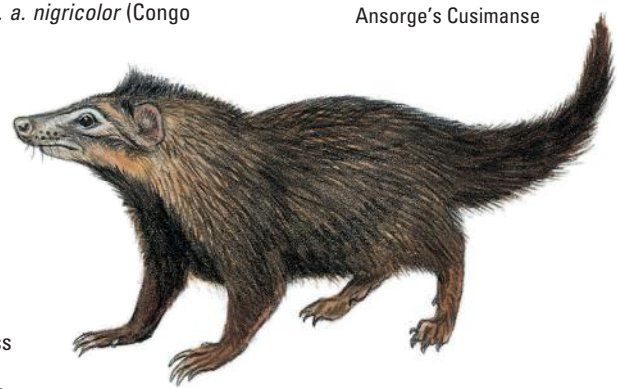
ANSORGE'S CUSIMANSE

Crossarchus ansorgei



Ansorge's Cusimanse

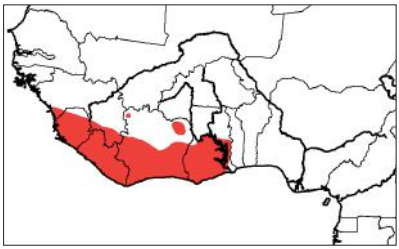
OTHER NAMES Angolan Cusimanse. Fr. *Mangue d'Ansorge*. Ger. *Angolakusimanse*.
MEASUREMENTS HB (est.) 320–360mm. T (est.) 200–220mm. W (est.) 0.6–1.5kg.
RECOGNITION A dark, forest mongoose with thick, brown fur on the body and dark brown or black limbs and tail. The muzzle is flat-fronted, blunt and shorter than in other cusimanses. The very dark Congo-basin form has conspicuous white flashes on the cheeks.
GEOGRAPHIC VARIATION *C. a. ansorgei* (Angola, northern escarpment zone), *C. a. nigricolor* (Congo basin, south of the river).
HABITAT Known only from high deciduous rainforest and said to avoid disturbed and cultivated land. Widespread and locally abundant in the central area of the Congo basin. In Angola, *C. ansorgei* is known only from one specimen.



FOOD Insect larvae, eggs and small vertebrates. Ansorge's Cusimanses are apparently less omnivorous than Alexander's Cusimanse (with which they co-exist) as newly captured animals absolutely refuse to take fruits, mushrooms or berries.
STATUS IUCN has recommended a survey of the Angolan population's status and the establishment of a protected area to conserve this and other N Angolan local endemics. Frequently found in Congolese bushmeat markets.

COMMON CUSIMANSE

Crossarchus obscurus



Common Cusimanse

OTHER NAMES Fr. *Mangue brune*. Ger. *Dunkelkusimanse*.
MEASUREMENTS HB 300–370mm. T 150–250mm. W 1.0–1.5kg.
RECOGNITION A tubby, long-nosed, strongly clawed mongoose. The paler underfur of the body is dense

and fine, with shaggy, very dark outer fur that gives it a rather unkempt appearance. The legs and tail have shorter fur while the head has a very short, sleek fur that is paler around the mouth. The nape is without whorls. It is noisy when disturbed. Small parties keep in touch with frequent chirps, churrs and twitters.

HABITAT Rainforest zone between Sierra Leone and Nigeria, where it inhabits the floor of the rainforest, notably in areas of dense undergrowth. It sleeps in burrows, in or under fallen logs, or in dense tangles.

FOOD Insects, earthworms, snails, myriapods, crabs and invertebrates generally; also mice, lizards, frogs, and other vertebrates and their eggs. The Common Cusimanse is said to kill rodents as large as a giant pouched rat *Cricetomys* cooperatively. Most food is found by excavating leaf-litter, dead wood and bark. A very quick and energetic forager, the Common Cusimanse also kills and chews its prey with great rapidity. It sometimes climbs in low trees and bushy tangles.

STATUS Common within its range, the Common Cusimanse is vigorously hunted. It is especially vulnerable to hunting with dogs, which may pose a threat in some localities. Overall, not endangered. IUCN lists as of least concern.

CAMEROON CUSIMANSE

Crossarchus platycephalus

OTHER NAMES Fr. *Mangue de Cameroun*.
Ger. *Kamerunkusimanse*.

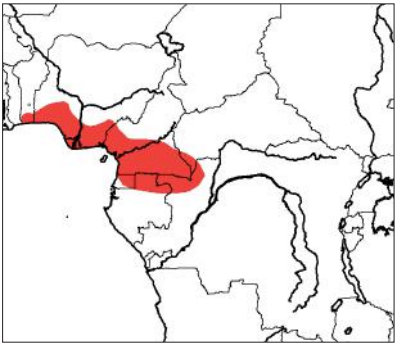
MEASUREMENTS HB (est.) 300–360mm.
T (est.) 150–250mm. W (est.) 1.0–1.5kg.

RECOGNITION A shaggy, forest mongoose, not easily distinguishable from the Common Cusimanse but with black guard hairs over a thick, brown undercoat. It is distinguished by the unusual breadth of the skull and by a crest arising between the ears and upper neck. It has usually been treated as a subspecies of *C. obscurus* but genetic studies support species status.

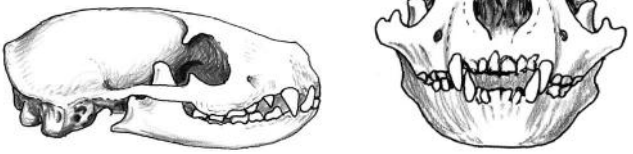
HABITAT Tropical rainforest between the Cross R. and Congo R. Very patchily distributed.

FOOD Forest floor invertebrates and small vertebrates.

STATUS Widely distributed but poorly known.



Cameroon Cusimanse



lateral (*right*) and frontal (*far right*) views of skull of Cameroon Cusimanse

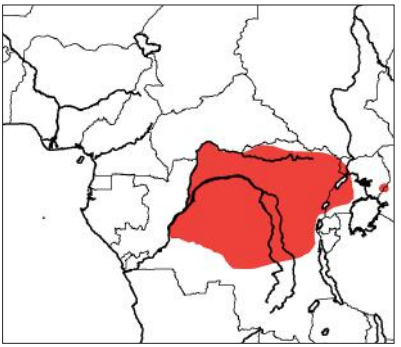
ALEXANDER'S CUSIMANSE

Crossarchus alexandri

OTHER NAMES Fr. *Mangue d'Alexandre*.
Ger. *Kongokusimanse*.

MEASUREMENTS HB 350–440mm. T 220–320mm.
W 1–2kg.

RECOGNITION A forest mongoose with a continuous crest running from crown to tail, thick, shaggy fur and a long-muzzled, short-furred face. The fur on the nape is conspicuously whorled in a curly cow-lick. This mongoose is a social animal that commonly



Alexander's Cusimanse

Alexander's Cusimanse

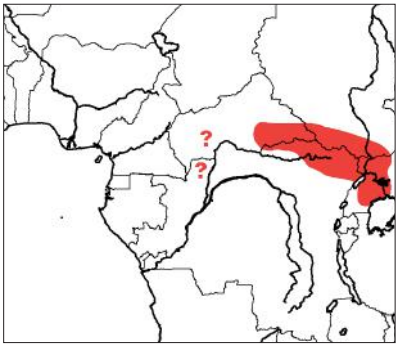
grunts and twitters while foraging. It is diurnal (but reputed to be at least partly nocturnal in Kivu). There are up to 20 animals in a pack.

GEOGRAPHIC VARIATION There are local variations in adult dimensions. Populations immediately south-west and east of Kisangani are substantially smaller in size. This difference is tentatively recognised as subspecific: *C. a. alexandri* (Congo basin), *C. a. minor* (Poke, Kivu and Uganda).

HABITAT Rainforest in Congo basin and W Uganda, where they favour damp valley bottoms and seasonally flooded swamp forest. A relict and possibly distinct population lives between 1,500 and 2,900m on Mt Elgon.

FOOD Earthworms, snails, slugs, beetles and other invertebrates; also small vertebrates and fallen fruits. These animals mainly forage in leaf-litter but will climb low trees and logs to dislodge insects, which they catch with great speed.

STATUS Mt Elgon population may be threatened by hunting. Overall, not endangered. IUCN status: least concern.



Savanna Mongoose

SAVANNA MONGOOSE *Dologale dybowski*

OTHER NAMES Pousargues's Mongoose.
Fr. *Mangouste de Dybowski*. Ger. *Listige Manguste*.

MEASUREMENTS HB 220–330mm. T 160–230mm. W (est.) 250–400g.

RECOGNITION A very small, grizzled mongoose with powerful claws on the forefeet and a thick, bushy tail. Body, tail and limbs are brown, the underparts are a warm, pale grey and the face is a darker grey. The throat displays a prominent reverse 'cow-lick' of fur. The Savanna Mongoose differs from the dwarf mongooses (*Helogale*) in having an undivided upper lip, a shorter palate and weaker teeth. It bears some resemblance to the Gambian Mongoose (*Mungos*) and to the cusimanses (*Crossarchus*) in teeth and skull. Its special interest as the likely relict of an earlier stage in the evolution of *Helogale* was mentioned earlier. *Helogale* resemblance is strong.

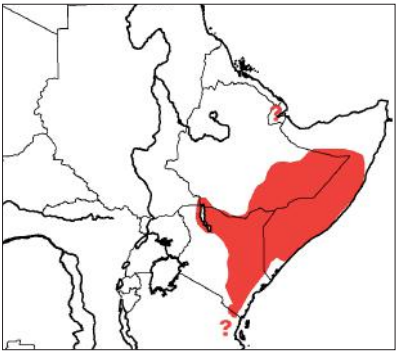
HABITAT Currently only known from moist savannas and margins of rainforest in NE DR Congo, South Sudan and NW and central Uganda. It may possibly range as far west as the Republic of Congo. It is thought to be diurnal and is associated with termitaries.

FOOD Unknown, but the long digging claws and unspecialised teeth of this species suggest fossorial invertebrates and small burrowing vertebrates.

STATUS The distribution of the very common Banded Mongoose is likely to considerably narrow the niche of this rare mongoose and study of its biology is an urgent precondition to understanding its status and how to conserve it.

SOMALI DWARF MONGOOSE

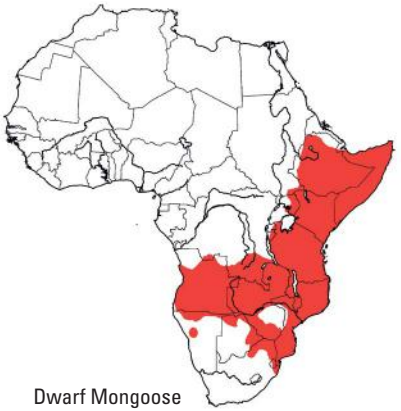
Helogale hirtula



Somali Dwarf Mongoose

OTHER NAMES Fr. *Mangouste velue*. Ger. *Somali Zwergichneumon*.
MEASUREMENTS HB (est.) 200–270mm. T (est.) 150–180mm. W (est.) 220–330g.
RECOGNITION A very small mongoose with longer, shaggier fur than the Dwarf Mongoose *H. parvula*. It also has more robust teeth. Colouring varies but is typically an overall grizzled grey with warmer-coloured underparts and face. The feet are dark brown. This is a social, diurnal species.
GEOGRAPHIC VARIATION *H. h. hirtula* (Somalia, Ethiopia, N Kenya), *H. h. percivali* (central and W Kenya).
HABITAT The Horn of Africa, mainly limited to a zone of bush, thicket and shrubby, deciduous woodlands dominated by *Acacia*, *Commiphora*, *Grewia* and *Cordia*. This species is able to live without water. Its habitat has been much modified by humans and their livestock, and would have been more densely wooded in the past.
FOOD Invertebrates and vertebrates of a similar range (but probably more arid-adapted) to that taken by the Dwarf Mongoose.
STATUS The entire range of the Somali Dwarf Mongoose overlaps that of the Dwarf Mongoose. The nature of their ecological separation or competitive exclusion awaits study.

DWARF MONGOOSE *Helogale parvula*


Dwarf Mongoose

OTHER NAMES Fr. *Mangouste naine*. Ger. *Zwergichneumon*. Swah. *Kitafe*.
MEASUREMENTS HB 180–280mm. T 140–190mm. W 210–350g.
RECOGNITION The Dwarf Mongoose is easily distinguished by its small size, rather infantile features, smooth, finely grizzled coat and its diurnal and social habits. The colouring is extremely varied, ranging from tan, yellowish and orangey red to dark brown and black. However, most individuals within a locality and a family party tend to have similar colouring.
GEOGRAPHIC VARIATION Variation has led to 17 subspecies being described. This classification is in need of revision, but three major divisions have been recognised: *H. p. parvula* (S Africa), *H. p. varia* (central Africa) and *H. p. undulata* (NE and E Africa).
DISTRIBUTION Warmer areas of East and central Africa below 2,000m; from Eritrea to Transvaal, west to Angola and Namibia. Effectively, they avoid highlands and forests.
HABITAT Savannas, thickets and woodlands, typically with numerous termitaries for shelter.

Dwarf Mongoose

Although they survive seasonally waterless periods, they are scarce in very arid, open country. They leave their marks in the form of communal latrines (generally a corner or crevice near a sleeping den). Sites are changed frequently.

FOOD Invertebrates, notably crickets and grasshoppers, termites, scorpions and spiders. Vertebrates comprise rodents (especially nests of young), lizards, snakes and birds. Dwarf Mongooses forage as a group, with a spread of some 50–60m, catching their prey by 'open' chasing and pouncing (not by stalking). They are able to follow some rodents down their burrows and have a substantial impact on rodent populations within their foraging area.

BEHAVIOUR This social species forms packs averaging over eight individuals (range 2–21), with more females than males and fluctuating numbers of young. The most frequent expression of sociality is mutual grooming, generally between same-sex pairs. Packs are strongly hierarchical, with a single dominant breeding pair. The pack is highly structured and led by a matriarch. The dominant male is particularly vigilant but immatures are also prone to scanning from elevated posts (this exposure leads to greater casualties among the males).

Infants are suckled by their matriarch mother or by other females that abort, lose or even lack having their own offspring. The young are cared for, fed and guarded by non-breeding adults of both sexes and there is intense competition to groom and carry infants. Litters are spaced 9–26 weeks apart and the privileged status of former infants is lost instantly on the arrival of new ones. After about 3 days of distress at their rejection, the initial generation become vigilant sentries, alert and nervous to everything around them. Older siblings help to bring food to infants, guard and retrieve them and huddle up to them at night or in cool weather.

Packs have territories that range from a very few hectares up to about 160ha (averaging about 35ha on the Serengeti Plains). The major landmarks in these territories are termitaries, to which all members flee if seriously disturbed. Overlaps in territory are very narrow and confrontations between packs are generally settled in favour of the larger group. While foraging, the group keeps in touch with a tinkling, vibrating chirrup. The most urgent warning cry is a shrill, explosive double note or shriek. A grating churr is directed at potential dangers on the ground, a shrill 'tchee' at any airborne threat. Anal marking or a plentiful cache of food elicits an outburst of shrill twittering. Distressed infants utter a twitter ending with a prolonged cheep, 'ti-ti-teee'. Group movements are begun with initiators making a scolding churr.

A matriarch can have up to three litters in succession, each of up to six young, spaced by a gestation period of 49–53 days, but major birth peaks occur during the rains. Young emerge from the termitary or den at about 4 weeks. At this time they are extremely playful and adults join them in wrestling, mock fighting and pouncing. This phase comes to an abrupt end with the arrival of the next litter, whereupon adult behaviour is acquired. Males that emigrate at this time have little chance of surviving but if they do they are the most likely males to become dominant. Dominance in both sexes is structurally linked with heightened fertility and with the survivorship of offspring.

ADAPTATIONS As the smallest of the mongooses, the Dwarf Mongoose has the most predators and must rely on termitaries for refuge and on a class of 'sentries' for early warning. Dens are often strategically sited near to bees' or wasps' nests, or even close to farm buildings (if there are no dogs present). Like monkeys, Dwarf Mongooses form mutually beneficial associations with hornbills. The hornbills catch disturbed flying insects and alert the mongooses to danger. Both species wait for one another and the birds are known to try to wake late risers by calling down their termitary chimneys. More one-sided relationships can form with larger mammals. Thus, Dwarf Mongooses have been seen to catch insects disturbed by a domestic bull and to use the bull as a perch and as a deterrent against potential predators. They are semi-immune to some poisons, notably scorpion venom, and to neurotoxins as found in cobras. They are more susceptible to the haemotoxins of adders, from which they occasionally die.

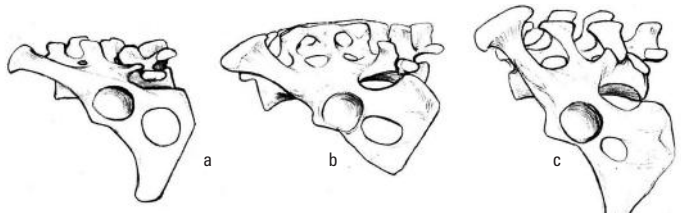
STATUS Not endangered. Listed by IUCN as least concern.

Highly specialised scaly ant-eaters, pangolins are typified by long, very muscular tails and horny scales over every outer surface, with only the face, throat, belly and inner limbs naked or covered in conventional mammalian hair. The scales were once thought to be cornified extrusions of the outer skin (or enlargements of the miniature scales that cover many rodent and insectivore tails). Since then it has been determined that the scales are essentially agglutinated hairs. It seems likely that a prehensile and abrasion-resistant 'fifth limb' was the primary adaptation of some arboreal, insect-eating proto-carnivore about 70 mya. Extending these scales to cover the rest of the body would have come later, after the protective function of a muscular, armoured tail had become well established. Such a history gains plausibility considering that no other mammal has more than the 47 tail vertebrae found in the arboreal Long-tailed Pangolin – sometimes described as 'a tail with ant-eater attached'. Descent from the trees and further dietary specialisation would have occurred much later. By about 45 mya recognisable pangolins inhabited Europe; a 35-million-year-old fossil from Mongolia is also unambiguously pangolin. The earliest fossil record for Africa (31 mya in Egypt) is of two bifid phalanges that are of typical pangolin structure. Clearly pangolins are an exceptionally ancient type of mammal.

Pangolin is a Malay name meaning 'one that rolls up' and, for defence, all species depend upon presenting a continuous sphere of overlapping armour when curled up into a tight ball. The top of the head is scaled but the tubular skull gains extra protection by being constructed of thick, dense bone. Pangolin heads are relatively small – mostly nose, with beady black eyes under swollen eyelids. Similar borders of thick skin surround open ear cavities (vestiges of ear cartilage under the skin indicate that pangolin ancestors had normal mammalian ears).

The small mouth is tucked in under the nose. Pangolins are toothless and have lost all capacity to chew, the lower mandible being no more than a hinged strut. Mastication is mimicked by cornified surfaces lining part of the muscle-encased stomach. The length of the tongue is as long as the head and body in African species. When not extended, the tongue, encased in a mucus-lined, eversible sheath, folds back into a throat pocket that visibly bulges and empties when the animal feeds. The tongue is very sticky and is served by enormous salivary glands so that forest species especially must drink frequently. The remarkable extensibility of the tongue is made possible through muscular action and its attachment, not to the hyoid as in other mammals, but to a very flexible prong that extends to the back of the abdominal cavity. This prong consists of the last pair of cartilaginous ribs, which, in pangolins, have become separated from their vertebral attachments and have joined up to form a free-floating extension of the sternum. The tongue's muscular extension runs the full length of this springy prong, allowing the worm-like tongue to travel right down termite holes and then whip back into the mouth smothered in insects.

In spite of their superficial resemblances to South American armadillos, pangolins evolved in the Old World along a separate evolutionary route, to arrive at parallel ant-eating specialisations.



Pelvis of (a) Tree Pangolin, (b) Giant Pangolin and (c) Ground Pangolin (not to scale).

PANGOLINS MANIDAE

Long-tailed Pangolin	*Uromanis tetradactyla*
Tree Pangolin	*Phataginus tricuspis*
Giant Pangolin	*Smutsia gigantea*
Ground Pangolin	*Smutsia temmincki*

RECOGNITION In spite of a similar armour of scales, pangolins are a very diverse group that range from 2kg arboreal species to the terrestrial Giant Pangolin weighing in at well over 30kg (fossil species were

bigger still). All species have sharp claws on the forefeet. These are used to open termite mounds and tear open hollow branches and trunks. They are also employed to some extent in male fighting and in defence. By contrast the hindlegs of light climbers and heavy walkers are much more divergent. In males the testes are contained in a superficial skinfold in the groin rather than in a true scrotum.

GENEALOGY Evidence from fossils suggests that divergence into various small/large, arboreal/terrestrial niches took place before pangolins spread from their place of origin, most likely tropical Asia.

GEOGRAPHY The four African and four Asiatic pangolins are remnants of a much larger radiation. European fossil genera include *Leptomanis*, *Necromanis* and *Teutomanis*. Other fossils include a more recent Indian form similar to the Giant Pangolin.

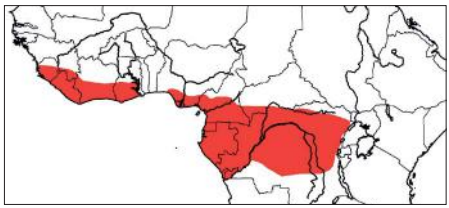
ECOLOGY The two arboreal species and the Giant Pangolin are strictly water-dependent and only occur in the moist forest belt in regions with very abundant ants and termites. The Ground Pangolin is more arid-adapted but only penetrates dry areas on the margins of its range in the Kalahari, Sudanic and Somali arid regions. All pangolins are almost exclusively feeders on ants and termites. These are consumed by attachment to the sticky surface of the tongue, swallowed and ground up with sand in the hardened gizzard-like stomach. All pangolin species can travel on the ground but the two arboreal species feed and sleep in rainforest trees. Both their bodies and their scales are appropriately light in weight. The much heavier terrestrial forms have dense, massive scales, reflecting more exposure to strong, well-armed predators.

NATURAL HISTORY Pangolins have discrete home ranges and males apparently defend well-marked territories that enclose the home-ranges of several females. Anal scent-gland marks, squirts of urine and faeces are deposited along well-used pathways and males commonly track down females by scent. More than one sleeping-place and several termitaries or ants' nests may be visited in a single night. The young are born in burrows or arboreal hollows and subsequently travel on their mother's tail. African pangolins normally have only one offspring at a time (Asiatic species are known to have up to three). All species can make hissing or puffing noises but they are mostly silent.

ADAPTATIONS In spite of huge differences in size and structure, all species depend upon rapid scissor movements of the tail during defence. In the smaller species this action cuts like a sharp-toothed saw while the larger species use the heavy blades of individual scales to wound an aggressor. In the case of the Giant Pangolin the entire tail may encircle an attacker's limb or it may lash out like a club. In the Ground Pangolin the tail acts as a counter-weight to the forequarters during bipedal walking or running. All pangolin species are victims of a rampant bushmeat trade that inflicts barbarous cruelty on these animals by hanging them alive, or half-alive, beside roadside stalls. It is symptomatic of the trade's exterminating rapacity that stalls that mostly sold buffalo, duiker and monkey meat a few years ago are now falling back on remnant species such as pangolins.

LONG-TAILED PANGOLIN

Uromanis tetradactyla



Long-tailed Pangolin

OTHER NAMES Fr. *Pangolin à longue queue*. Ger. *Langschwanzschuppentier*.

MEASUREMENTS HB 280–340mm. T 550–800mm. W 2.2–3.6kg.

RECOGNITION A small, arboreal pangolin with a very long tail, black face and underparts. The muzzle is naked and pointed. The scales, which are relatively broad and only reveal the faintest of striations, have brown bases with light-yellow margins. The Long-tailed Pangolin is active by day and also by night but very wary and difficult to see.

DISTRIBUTION All permanent rivers on the Atlantic coast from Senegal to W Angola, especially the Congo R. throughout its lowland basin.

HABITAT Very localised; never far from permanent water and watercourses, preferring riverine and swamp forests. The Long-tailed Pangolin sleeps in tree hollows or in hollowed-out insect nests.

FOOD Tree ants (*Crematogaster* and *Cataulacus*), which occur in swampy areas, are the favoured food. These are eaten on branches or broken out of their arboreal nests and hollows.

BEHAVIOUR This species uses habitual routes and sleeping-holes in a well-known home-range. It follows urine and anal scent-gland trails (urine and anal secretions are also expelled in order

to discourage predators). Breeding is non-seasonal and almost continuous as the female conceives again within 2 weeks of birth. Gestation is estimated at about 140 days. The single young is born in a hole where it may be left during its first week while the mother forages. Thereafter it clings to the mother's rump or tail and begins to glean ants at about 2 weeks. It departs at the birth of a new infant and wanders for 4 or 5 months before settling down into its own home-range.

Long-tailed Pangolin

ADAPTATIONS A long, prehensile tail is likely to have been one of the primary adaptations of proto-pangolins. Its use as a versatile third limb is demonstrated when the pangolin descends large tree trunks in a shallow, tail-clinging spiral and during copulation, when both animals entwine. This species is markedly shyer than other pangolins and shows faster responses in enclosing itself within its tightly wound tail at the least alarm. The tip of the tail has a naked, finger-like pad, which is highly sensitive.

STATUS Because it is small and shy and inhabits a type of forest that is forbidding (full of biting ants and frequently very thorny), it is seldom seen. Such habitats are currently the least at risk and arboreal pangolins are more secure than the two terrestrial species.

TREE PANGOLIN *Phataginus tricuspis*

OTHER NAMES African White-bellied Pangolin. Fr. *Pangolin commun*. Ger. *Weissbauchschuppentier*. Swah. *Kakakuona ya miti*.

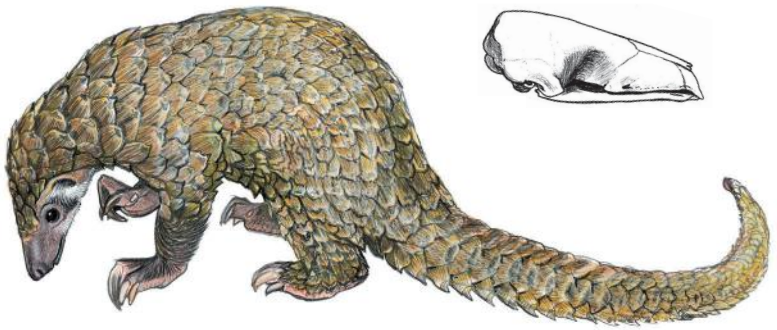
MEASUREMENTS HB 250–430mm. T 350–620mm. W 1.6–3kg.

RECOGNITION A small, arboreal pangolin with very numerous, thin scales, resembling fir-cone scales in texture but with serrated ('three-cusped') points. Old animals have elongated, less striated scales with abraded ends. The muzzle is thicker and shorter than that of the Long-tailed Pangolin and the skin is much paler, with sparse white fur on the belly and browner hair on the limbs and neck. The tail is tipped with a sensitive, thumb-like pad.

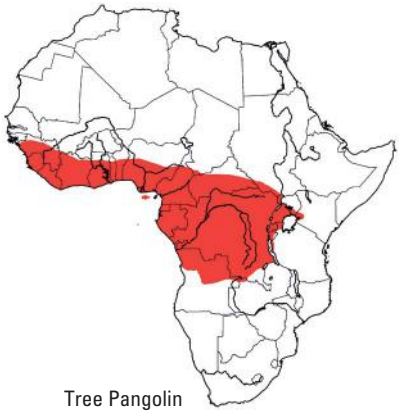
GEOGRAPHIC VARIATION None named but animals from Upper Guinea are smaller.

DISTRIBUTION Senegal to W Kenya and the Congo basin to N Angola and Zambia.

HABITAT All through the lowland rainforest block (and many outliers) but especially favours secondary growth, surviving quite well in cultivation, fallow and forest mosaics.



FOOD Mainly termites, notably *Nasutitermes* and *Microcerotermes*, which are mostly found on the ground; also ants (*Dorylus* and *Myrmecaria*). Although the Tree Pangolin opens up decayed bark and small termite mounds, most foraging is on the surface and in leaf-litter. The tail sometimes helps sweep insects within range of the flickering tongue. In keeping with the termites' activity cycle, this pangolin is predominantly nocturnal, females feeding in bouts of 3 or 4 hours while males travel further and only rest after 5 or 6 hours. Scent trails help females to avoid contact with one another while foraging.



Tree Pangolin

BEHAVIOUR Adult females are highly sedentary and sleep in self-dug holes that are used for long periods. They forage over a few hundred metres within overlapping home-ranges of some 3 or 4ha. Adult males are more nomadic, moving about a kilometre or more within territories of up to 30ha. They tolerate and regularly monitor all the adult females within their range but expel offspring as they mature. Although some sleeping-holes are excavated in arboreal termitaries and hollow trunks, most are dug at or near ground level. Gestation is estimated at about 150 days and a single infant is born in the mother's hole (where it is only left for very short periods). The baby begins to travel perched on its mother's tail at 2 weeks and mother and young forage together for up to 5 months. Adult size is not reached before 15 months. Animals are sexually mature by 8 months.

ADAPTATIONS Equally at home in trees and on the ground, this species is the most versatile and therefore the most common and widespread of the forest pangolins.

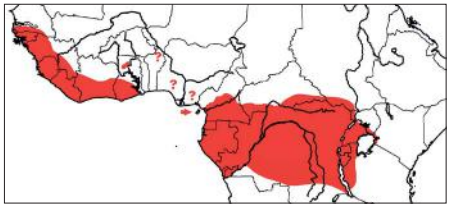
STATUS High fecundity and a mixed diet of termites and ants allows the Tree Pangolin to offset heavy predation in some areas (including high levels of both internal and external parasites). Currently one of the commonest victims of the appalling bushmeat trade and routinely subjected to mindless cruelty.

GIANT PANGOLIN *Smutsia gigantea*

OTHER NAMES Fr. *Pangolin géant*. Ger. *Riesenschuppentier*. Swah. *Kakakuona mkubwa*.

MEASUREMENTS HB 750–1,000mm. T 500–700mm. W 30–35kg.

RECOGNITION The largest and heaviest of living pangolins, this powerfully built animal has a highly precise and geometric pattern of brunette scales that darken and change both texture and shape with age. With wear and tear, the regular symmetry of scaling is also obscured in old individuals. The hindlegs leave prints that resemble those of a small elephant. At the front, weight is taken on the wrist, with long sharp claws folded inwards and facing to the rear. The tail, unlike that of the Ground Pangolin, often leaves a heavy drag mark. The tubular snout is appreciably longer and less tapered than that of the Ground Pangolin.

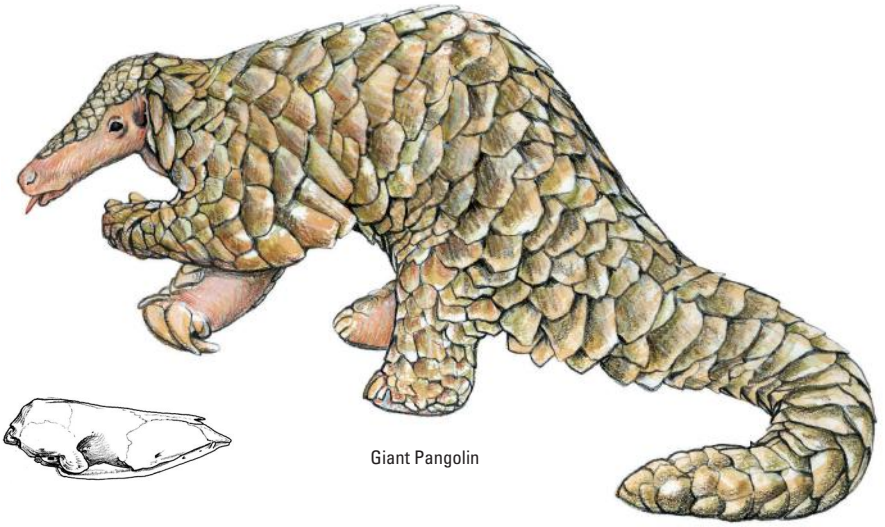


Giant Pangolin

DISTRIBUTION From Senegal to Togo and Cameroon to W Kenya (north of the R. Kasai and R. Tshuapa). Sightings reported from Angola and the Udzungwa Mts in Tanzania might be misidentified Ground Pangolins.

HABITAT Mainly forest and forest mosaics but survives in high-rainfall secondary grasslands where it can shelter in thicket-covered termitaries. It is totally water-dependent. It may use the burrows of other animals but also digs long deep burrows, up to 40m long and 1.5m deep. Entrances are usually plugged from within. It also rests up under fallen tree roots, thicket tangles and piles of plant debris.

FOOD Termites, notably *Macrotermes*, *Cubitermes*, *Apicotermes*, *Protermes*, and ants, such as *Palthothyreus* and *Anomma*. Other insects and larvae are also taken. Even water-beetles (*Dytiscidae*) are licked off the surface of pools (the Giant Pangolin is an able swimmer). Most



Giant Pangolin

feeding takes place between midnight and dawn but seasonal differences are likely. Frequent periods of inactivity, sometimes very prolonged, suggest that this large ant-eater can survive periods of acute shortage by a form of aestivation but makes up for this with periods of glut and storage of body fat.

BEHAVIOUR Solitary and well-spaced, the enlarged anal glands and greater marking activity of the heavier males suggests that they are intolerant of other males. Individuals have been known to inhabit a very limited locality for up to 2 years but their seasonal and overall ranges are poorly known. Gestation has been estimated at about 5 months and a single open-eyed young is born with soft, amber-coloured scales that harden rapidly. Beginning to feed on ants by 3 months, the young accompanies its mother until the next infant is born.

Because it is shy and nocturnal, most diurnal animals, including humans, are unfamiliar with *S. gigantea*. This fact brings an interesting dimension to an incident in a stony valley in Mahale NP in Tanzania. Hearing a group of Common Chimpanzees in a state of noisy excitement one morning, observers found the apes clustered around the freshly killed body of a Giant Pangolin. At the scene, abandoned stones and the pangolin's cracked skull suggested it had been killed by the apes and that the stones had been used as weapons.

ADAPTATIONS The spread-eagled agility, strongly prehensile tail and strong clinging reflexes of the newborn are clear indications of the arboreal origins of this heavy terrestrial pangolin. A highly localised distribution implies the need for a large and sustained biomass of ants and termites. It has been recorded as taking up to 2 litres of insects a night.

STATUS The use of scales as love-charms and a widespread taste for their meat (a special delicacy in Gabon) has led to much local depletion or extinction. Formerly protected in some areas as a totemic species (i.e. for the Olugave clan in Buganda), the breakdown of such taboos now permits interference. Mostly rare and widely vulnerable.

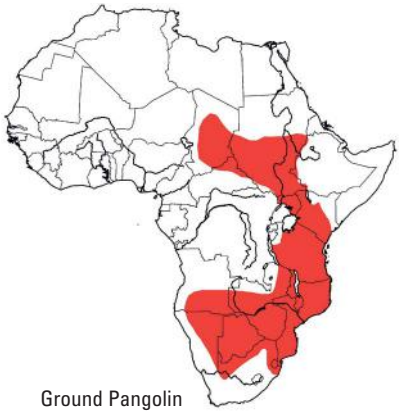
GROUND PANGOLIN *Smutsia temminckii*

OTHER NAMES Fr. *Pangolin de Temminck*. Ger. *Steppenschuppentier*. Swah. *Kakakuona*.

MEASUREMENTS HB 340–610mm. T 310–500mm. W 7–18kg. (males up to 50% heavier than females).

RECOGNITION A rotund pangolin with broad, rounded scales and heavy, graviportal hindlegs. The forelegs, although strong, are proportionately less massive than those of the Giant Pangolin. The tail is very broad, with a concave lower surface, and is shorter than that of other pangolins.

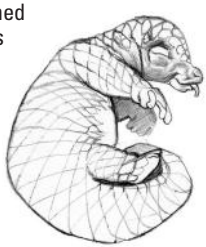
DISTRIBUTION From L. Chad, north of the R. Ubangi to S Kordofan and the upper Nile Valley (but absent from Ethiopia and Somalia). Also east of the Victoria Nile and L. Victoria to L. Malawi (L. Nyasa). In subtropical southern Africa it is found in Angola and there is an undetermined distribution in Mozambique (possibly separated into southern and northern populations).



Ground Pangolin

HABITAT Occurs in both high- and low-rainfall areas with both sandy and rocky soils, in woodlands, savannas and grasslands. The main determinant of this species' range is an abundance of ants and termites of a few specific types. A scarcity or absence of these explains its absence from Ethiopia and may also account for its absence west of L. Chad (other ant-eating animals are also absent from W Africa).

FOOD Mainly ants, including the genera *Anoplepis*, *Paltothyreus*, *Camponotus* and *Crematogaster*. Some of the most commonly eaten ants are tiny, colony-living species. Less frequently taken are certain termite genera: *Odontotermes*, *Microcerotermes*, *Ancistrotermes*, *Amitermes* and *Microtermes*. The Ground Pangolin forages very slowly, often 'freezing' and only making shallow, cup-like excavations, moving the soil slowly and carefully so that the tongue can flick in and out of the ants' passages. It tends to feed intensively for about 15 seconds and then depart abruptly. A sucking sound is made by the rapid extrusion and return of the sticky tongue. Other small insects, such as dung-beetle larvae, are also eaten. It sometimes takes loose pieces of termitary, broken wood or dry elephant dung in its forepaws and, rolling onto its back, licks the insects off as the object is manipulated or broken up. Activity is determined by whether prey species are on or near the surface; thus most feeding is nocturnal during the dry season, but may become diurnal in other seasons. Young animals tend to forage for a longer period than adults.

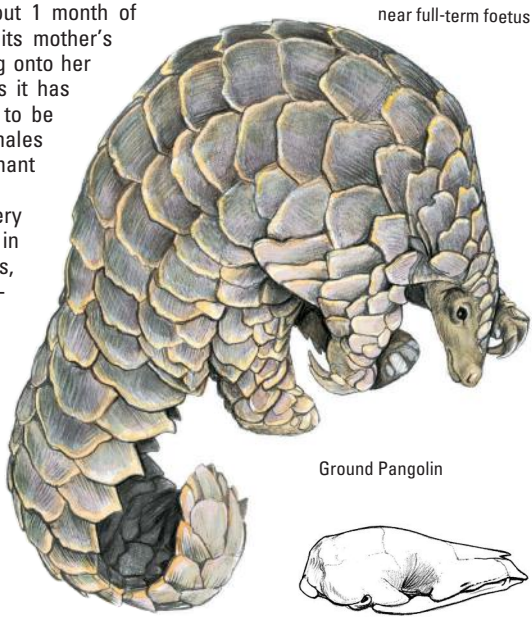


near full-term foetus

BEHAVIOUR Although capable of digging a burrow, the Ground Pangolin prefers to use natural shelters or disused holes of other species. It is a slow but capable climber, using sharp points along the margins of the tail to gain purchase on bark or soil. During the rains it can create a shallow wallow by gyrating backwards in a tight circle so that water collects. Only one young is born at a time after a gestation estimated at 130–150 days. After about 1 month of limited activity the young travels on its mother's back or on the root of her tail (slipping onto her belly at the least alarm). By 3 months it has begun to feed on ants but continues to be carried until it weighs about 3kg. Females breed continuously and become pregnant again while still with a small offspring.

ADAPTATIONS The Ground Pangolin is very frequently bipedal and this is reflected in the structure of its pelvis, broad hips, relatively short heavy tail and kangaroo-style carriage of the forepaws (tucked in close to the chest).

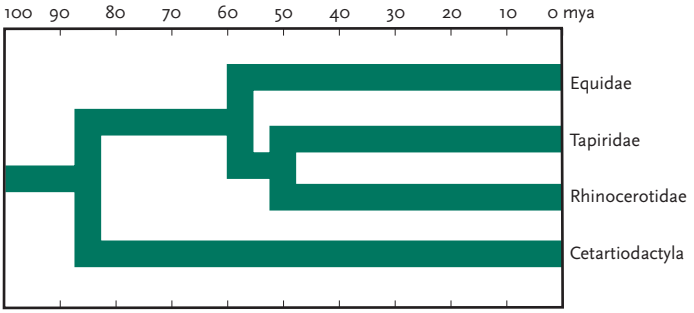
STATUS The Ground Pangolin has been exterminated in many parts of its overall range by hunting for both its flesh and scales, which are used as love-charms. It is attacked by Lions and hyaenas, frequently burnt in bush fires, and faces new dangers in the form of pesticides laid down for locusts and electrocution in places where electric fences are employed.



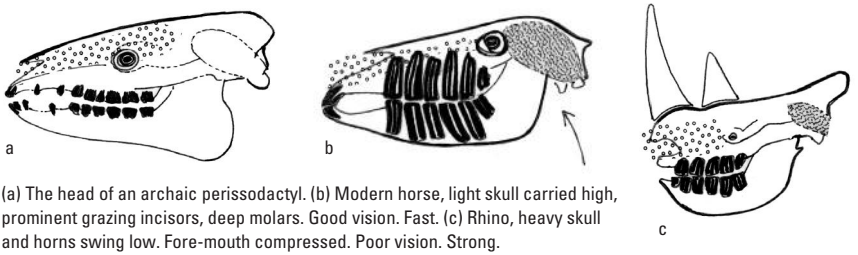
Ground Pangolin

Horses	Equidae
Rhinoceroses	Rhinocerotidae

The earliest forms of Perissodactyla ('odd-toed ones') had five toes on both fore- and hindfeet. They emerged from a primitive ungulate, typified by 57-million-year-old *Radinskaya*, fossils of which were first found in Mongolia in 1989. By 55 mya these early forms had already diversified into different adaptive niches. Five toes have been progressively reduced through time to three in rhinoceroses and one in horses (equids). Excellent fossil series document the progression and show that this evolution took place outside Africa. The fossil evidence suggests that this group diversified in America and Eurasia to become the most abundant of herbivores between 55 million and 34 mya. They retain a superior ability to digest coarse fibrous vegetation. Modern rhinos emerged in Eurasia and North America about 40 mya. The ancestral single-toed equine *Dinohippus* emerged about 12 mya; the genus *Equus* not more than 4–5 mya.



Tentative phylogenetic tree of Perissodactyla (after Bininda-Emonds *et al.* 2007, Meredith *et al.* 2011)

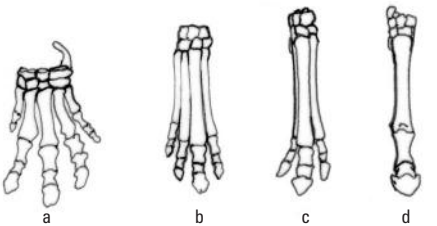


(a) The head of an archaic perissodactyl. (b) Modern horse, light skull carried high, prominent grazing incisors, deep molars. Good vision. Fast. (c) Rhino, heavy skull and horns swing low. Fore-mouth compressed. Poor vision. Strong.

HORSES EQUIDAE

Equids evolved in North America, where well-dated and well-preserved fossils record their evolution from a small, duiker-like forest animal called the 'dawn horse', or 'Eohippus'. Many of the early forms were browsers but one lineage adapted to a diet of tougher vegetation and to drier, harder soils under foot.

Modern horses and zebras mostly differentiated in North America from about 5 mya to 3 mya and were so versatile and successful that they reached Asia and, eventually, Africa (their niche, before then, was occupied by three-toed hipparions which arrived in Africa 10.5 mya.) For at least half a million years (2.3 to 1.8 mya) abundant fossils of equines called *Equus oldowayensis*, *E. koobiforensis* and *E. capensis* indicate these were very common and widespread equines. Earlier still, fossils of *E. sanmeniensis* in China and *E. stenonis* in Eu-



(a) Protoungulate (*Phenacodus*). (b) Primitive perissodactyl (*Hyracotherium*). (c) Early horse (*Miohippus*). (d) Modern horse (*Equus*).

rope imply that these antecedents of the *E. grevyi* lineage had the most extensive history as modern equines. Common Zebras, Mountain Zebras and African Wild Asses followed (or evolved later) in a staggered sequence that has yet to be settled.

AFRICAN HORSES *Equus*

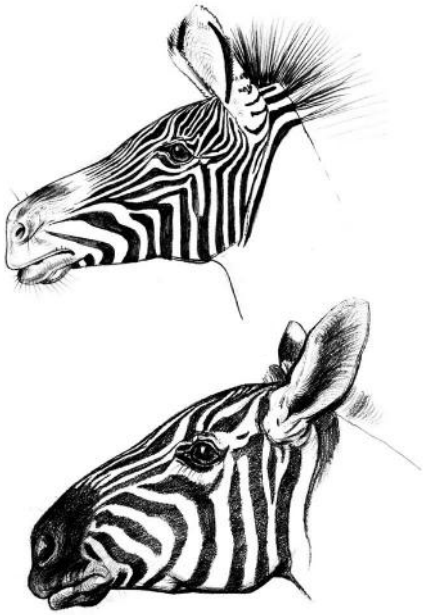
Grevy's Zebra	*Equus grevyi*
Common Zebra	*Equus quagga*
Mountain Zebra	*Equus zebra*
African Wild Ass	*Equus africanus*

African horses (asses and zebras) are all partially or wholly striped and all have a short, sleek coat. All have a big, long head, with large, flat chewing muscles over deeply rooted tooth-rows. The neck is muscular and maned and the body is compact with a deep chest and very muscular haunches. The legs are strong and bony, with hard, single hooves. All equids can be very vocal, with a variety of neighs, barks or brays, squeals and whinnies.

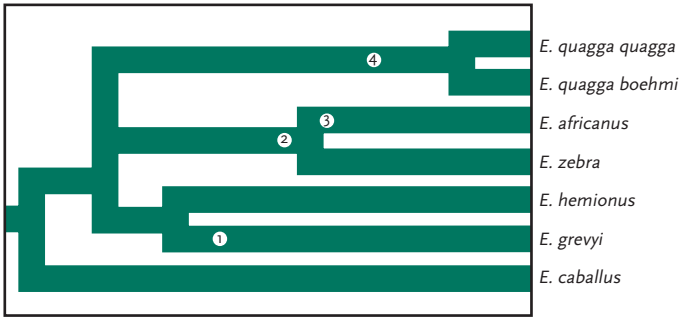
Only the most successful of the horses, those able to compete with ruminants, found their way to Africa, via Asia, from North America. Both the Common and Grevy's Zebras evolved their basic adaptive specialisations outside Africa. The present distributions of all equids are only vestiges of their past ranges, for example *E. quagga* was once found on grasslands all over Africa and, very likely, *E. grevyi* before that.

Zebras are high-density, tropical grassland equids. Asses are low-density, desert-adapted forms. Their ability to digest tough, unpalatable grasses and move quickly between pastures is not matched by any bovid. Nor is the speed of their digestion.

Equids are extremely flexible, easily dispersing as small units or joining up in very large aggregations. The basic unit of a female and her young may acquire a permanent attendant male that is equally mobile or they may move in or out of male territories. All equids keep their coat in condition by dust-bathing, rolling, rubbing and some mutual nibbling. The stripes of zebras appear to serve as a visual bonding device. It is known that evenly spaced, black and white bars stimulate visual neurones very strongly and the



Heads of Grevy's Zebra (*above*) and Common Zebra (*below*).



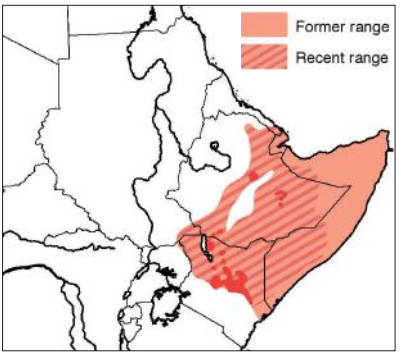
Tentative phylogentic tree of extant equids (after Orlando *et al.* 2009). Numbers indicate likely sequence of arrivals in Africa.

zebras' stripes appear to make them super-attractive to one another. The aggressively anti-social behaviour of territorial animals would thus appear to be counter-acted, or at least modified, by visual attractiveness. Notwithstanding this, both males and females are mutually antagonistic and even young foals (the most social class) sometimes prefer members of the opposite sex.

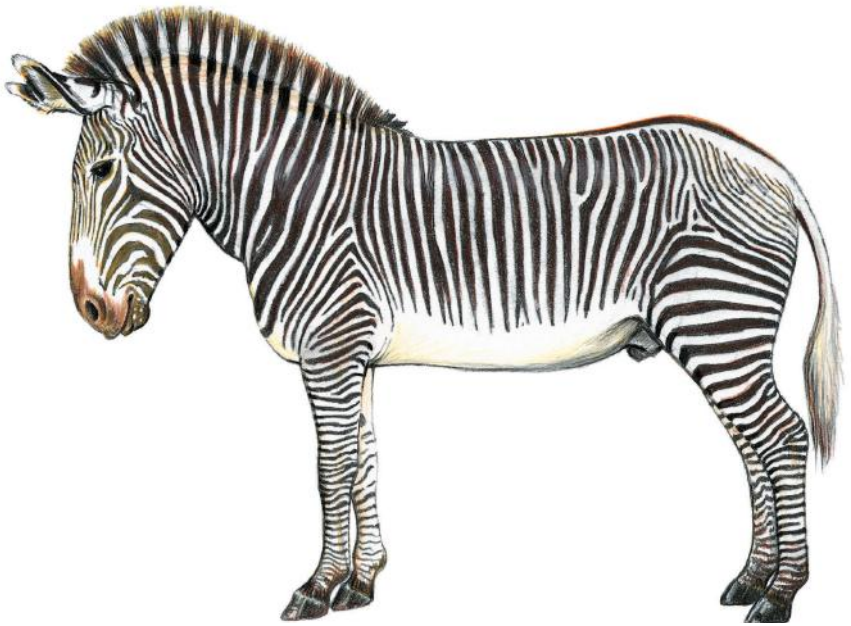
A short, sleek coat is required in order to produce the crisp edges necessary for a striking visual pattern such as the zebras' stripes. Thick, shaggy coats required in cold climates subvert this. Striping was therefore absent or vestigial in temperate equids and in the Quagga (now extinct), a population that survived cold winters in the Karoo by growing a winter coat. Likewise the value of striping as a visual bonding system is greatly reduced when an equid is at low densities with infrequent gatherings. Thus, although African Wild Asses show vestigial patterns on legs and neck, they otherwise match their tawny-grey surroundings.

GREVY'S ZEBRA *Equus grevyi*

OTHER NAMES Imperial Zebra. Fr. *Zèbre de Grévy*. Ger. *Grevyzebra*. Swah. *Punda milia ya Yohannes*.
MEASUREMENTS HB 2.5–3.0m. T 400–750mm. Sh. ht 1.4–1.6mm. W 385kg (350–400kg) (♀), 430kg (380–450kg) (♂).
RECOGNITION A long-legged, long-faced zebra with broad, rather ovoid ears, a stripeless white belly and a white-margined spinal stripe. The stripes are very uniformly distributed over the body, head and limbs but overall widths vary so that there are lighter and darker individuals among the 'even' majority. The type specimen was a live diplomatic gift, offered in 1881 to France by the Emperor of Ethiopia (seeking support against Italy). Accepted by the then French President, Jules Grevy, its earliest vernacular name, the 'Imperial Zebra', honoured Emperor Yohannes IV, the donor, not Grevy, the political recipient. The Imperial Zebra was the 'Hippotigris' that was paraded in Roman circuses in AD 211–217, pulling



Grevy's Zebra



Left: Ear signals in Grevy's Zebra.
Below: Grevy's Zebra braying.

carts.

DISTRIBUTION The immediate historically known distribution of *E. grevyi* included a large part of the Somali arid zone, the Ethiopian Rift Valley, the Awash Valley and Danakil depression. However, numerous fossils from Asia and Africa suggest that ancestral forms, or proto-*E. grevyi*, were once successful and widespread in Eurasia and Africa. At the present time they occur in a few reserves and parks in Ethiopia and Kenya. They are no longer found in Somalia, Djibouti, Eritrea, Karamoja or southern Sudan.

HABITAT Bush/grass mosaics with a preference for tracts of grassland growing on deep sand, hard-pans, sumplands and in areas where fire and elephants have degraded the dominant *Acacia/Commiphora* woodlands. Seasonally waterlogged plains are extensive in parts of its range and gatherings of thousands of zebras were once seen on such grasslands in the past. It associates with Giraffes, oryxes, elands and, in the southern part of their range, with Common Zebras, Impalas and African Buffalos. An individual's long-term range covers many thousands of kilometres.

FOOD Grevy's Zebras benefit from the spread of a grassland type dominated by *Pennisetum schimperi*, a tough grass incompletely exploited by other grazers. Other important grasses in the diet are species of *Chrysopogon*, *Cenchrus* and *Enteropogon* but it grazes many other genera as well.

BEHAVIOUR These zebras have an open society in which females with their young and males on established territories (of up to 12km^2) are the stable foci. Females associate in nursing groups, males in bachelor groups and all classes may join up in large, mixed herds. Aggression is inconspicuous except that territorial males assert their mating prerogatives. The most successful males win grassy territories close to water. Grass and water are major attractions, especially for lactating females.

Resident stallions actively seek the company of visiting females. Dominance is asserted by a proud posture, with arched neck and high-stepping gait. Submission is signalled by a lowered head and raised tail. While courting and copulating the male utters a very loud bray followed by a long, strangulated squeak. Both females and males tend to appease the caller. A single foal is born after a variable but exceptionally long gestation of about 400 days (55–61 weeks). Mothers return to very localised birthing areas that appear to be traditional. The new foal has a mane running from forehead to tail and another hairy tract along the centre of its belly. Both are shed as the foal grows up but the dorsal mane elicits direct contact from the mother. The brown-and-white baby colouring darkens first on the neck and ears and a woolly coat then gives way to sleek black and white. Foals follow every detail of their mother's course and often suckle from behind. Rapid tail-lashing precedes threat and brings a foal close to its mother's side. Mothers can be in milk for up to 12 months but the young take their first water at 3 months and some cease suckling after 6 months. In spite of remaining with their mothers for up to 3 years, colts can be relatively independent at 7 months. Wild zebras mature and breed later than in zoos, where births at 3–5 years are not uncommon. Females

and males tend to breed in the wild closer to 6 years. They live for up to 31 years.

ADAPTATIONS The wide scatter of fossils belonging to this lineage and lack of any very obvious specialisation suggests that it is the relict of an early, pioneering, once widespread generalist. If competition from other equids has been an influence it may be significant that the distribution of Grevy's Zebra is wedged between the ranges of the arid-adapted African Wild Ass and the water-loving Common Zebra. There are superficially similar habitats south of the Sahara and the Kalahari, where competition from semi-arid adapted grazers (such as the Hartebeest, Roan Antelope and other zebra species) would be plausible in explaining a naturally contracting range. Extensive travel over poorly known terrain, a slow birth rate, limited ability to go without water (about 5 days), as well as the attachment of males to territories, all work against this species. As in the past, Lions are contributing to attrition of the last populations in Kenya.

STATUS This species has seen one of the fastest contractions in range and numbers of any large African mammal. Known to have declined over most of its range throughout the present century, a 1977 estimate of 13,700 animals in Kenya was followed by an estimate of 4,276 in 1988, a decline of 70% in 11 years. At last count the world population was 2,700 individuals, and fewer by the day. The primary threat has come from ever-increasing livestock, leading to the zebras' exclusion from traditional watering places. Formerly nomadic people have settled around these sources of water or above new bore-holes within good grazing areas. Limited sources of grazing are put under increasing pastoral pressure, especially by sheep and goats. Up-stream irrigation is causing reduced flows in the lowlands with further reductions in the water available to the zebras. About 550 animals are held in zoos and most are managed in a species survival programme. IUCN lists this zebra as endangered.

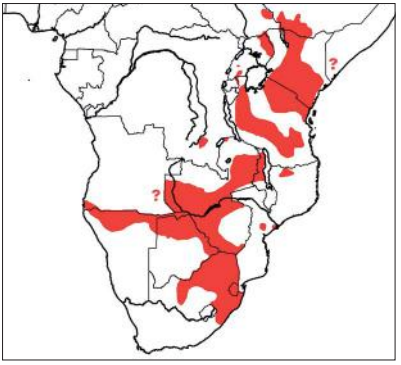
COMMON ZEBRA *Equus quagga*

OTHER NAMES Plains Zebra. Fr. *Zèbre de steppe*. Ger. *Steppenzebra*. Swah. *Punda milia*.

MEASUREMENTS HB 2.17–2.46m. T 470–570mm. Sh. ht 1.27–1.40m. W 175–250kg (♀), 220–322kg (♂).

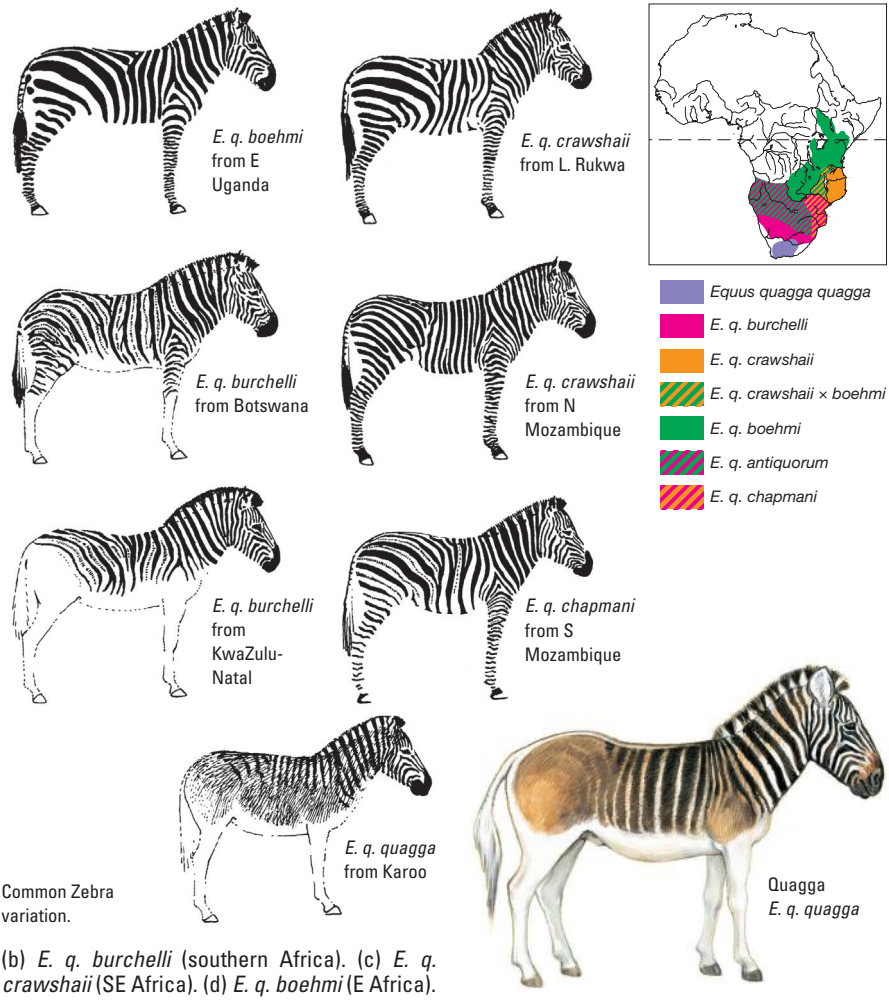
RECOGNITION A muscular equid with relatively short neck and sturdy legs. The stripes are subject to much regional and individual variation. Patterns are better illustrated than described (see figure overleaf).

GEOGRAPHIC VARIATION Four regional foci with several intermediate/variable types coming from inter-zones, some of which seem to be very extensive. (a) *E. q. quagga* (Cape, Karoo) extinct.



Common Zebra

Mozambique Common Zebra
E. q. crawshaii


E. q. boehmi from E Uganda
E. q. crawshaii from L. Rukwa
Equus quagga quagga
E. q. burchelli
E. q. crawshaii
E. q. crawshaii × boehmi
E. q. boehmi
E. q. antiquorum
E. q. chapmani
E. q. burchelli from Botswana
E. q. crawshaii from N Mozambique
E. q. burchelli from KwaZulu-Natal
E. q. chapmani from S Mozambique
E. q. quagga from Karoo
Quagga
E. q. quagga

Common Zebra variation.

(b) *E. q. burchelli* (southern Africa). (c) *E. q. crawshaii* (SE Africa). (d) *E. q. boehmi* (E Africa).

Intermediate/variable populations commonly given subspecific ranking: *E. q. antiquorum* (SW Africa, appears to combine *burchelli* and *boehmi* features). *E. q. chapmani* (ex *selousi*) (southern SE Africa, combines *burchelli* and *crawshaii* features). Intermediates between *boehmi* and *crawshaii* occur in the Rukwa/Usangu area.

DISTRIBUTION Formerly inhabited all of non-forest, non-desertic Africa (e.g. it appears to have occupied Algeria for 2 million years). In historic times limited to southern and East Africa east of the Nile and south of the Congo basin.

HABITAT Grasslands, steppes, savannas and woodlands. These zebras are totally dependent on frequent drinking. They prefer firm ground underfoot so may move off sumplands during flooding.

FOOD Grass of the most available species. Adaptable grazers, they mow short lawns close to the roots but are equally able to take taller flowering grasses. Water shortage may concentrate zebra populations around available waterholes during the dry season. Daily activity is dominated by shifts from open night-time resting areas to pastures, to water and back to sleep or rest.

BEHAVIOUR Up to six females and their young live in very stable 'harems' where they are subject to low-key but continuous coercion by the harem stallion. He herds the females in his group whenever they stray and threatens males that come too close. The number of females appears to be limited by the intolerance of established females against incomers.

Common Zebras are extremely vocal, the adult males being particularly noisy during any nocturnal movement. For each social unit the stallion's individual 'song' (a glottal, barking bray) becomes the focal point for all harem members. Individuals that become separated from their group seek it with every sign of distress while the stallion too calls and searches until the group is reunited. Normally only harem stallions mate with harem mares but neighbours and bachelor groups show intense interest in any oestrous females. One foal (rarely two) is born after a 12-month gestation. Foals suck milk for up to 6 months but begin to graze in the first month. They are sexually mature by 18 months to 3 years but females cycle without conceiving for a year or two and males seldom acquire harems before 5 years of age. Common Zebras are known to live for 40 years.

ADAPTATIONS Mutual nibbling of the legs, shoulders and neck is the main form of social contact within Common Zebra families. It is most conspicuous and frequent between mothers and their young and between similarly aged foals. This direct contact tends to diminish with age. The movements of champing the jaws and nodding the head frequently become detached gestures that are made close to a potential grooming partner but without actually touching. Unstriped equids retain nibbling as a mode of bonding between adults. The difference may concern stripes, which are thought to facilitate bonding in adult zebras (see genus profile above). One-to-one physical bonding seems to develop into multi-partner 'visual bonding' through a form of conditioning or habituation. By experiencing very strong optical stimulation in the context of close contact and security the foal thereafter seeks to maintain that security by remaining close to stripes.

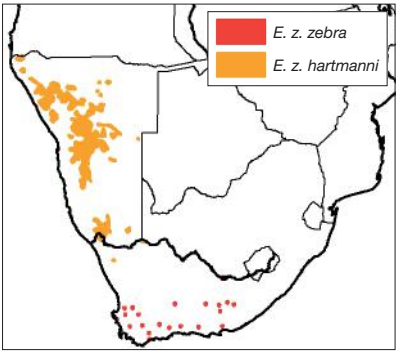
STATUS The incompatibility of zebras with modern agriculture and ranching has led to their extermination over many areas. It is a process that continues unabated outside national parks. Given the uncertain future of small, isolated populations, some local forms of Common Zebras, such as *E. q. borensis*, even *E. q. crawshaii*, could become vulnerable. IUCN rates the species as of least concern.

MOUNTAIN ZEBRA *Equus zebra*

OTHER NAMES Fr. *Zèbre de montagne*.
Ger. *Bergzebra*.

MEASUREMENTS HB 2.2–2.6m. T 400–550mm.
Sh. ht 1.46m (1.15–1.50m). W 275kg (230–320kg) (♀), 300kg (250–386kg) (♂).

RECOGNITION Evenly spaced, vertical, black-and-white stripes on neck and body with a sudden 'change of scale' to three or four very bold, horizontal stripes on hindquarters. The body stripes extend into an enclosed 'grid-iron' pattern on the rump and upper tail. The legs have fine, even, black-and-white striping. Black stripes on the face graduate to orange-brown on the bridge of the nose and around the mouth and nostrils (which are dark brown). The ears are moderately long and broad, their backs marked with bold black-and-white patches. Striping in the tall mane and over a dewlap enlarges the visual impact of the neck, especially in adult males (making them look 'front-heavy'). Hooves grow exceptionally fast, leaving a characteristic hard-edged, rounded spoor.



Mountain Zebra

GEOGRAPHIC VARIATION Cape Mountain Zebra, *E. z. zebra* (Cape and Karoo); Hartmann's Mountain Zebra, *E. z. hartmanni* (S Angola to Orange R.). (The smaller Cape race averages 50kg lighter.)

DISTRIBUTION Arid mountains and escarpments sufficiently close to the ocean to catch mist and cloud (and thus have springs and water sources) in a long band running from SW Angola to the mountains of the Cape and Karoo.

HABITAT Formerly widespread in bushy Karoo shrubland in uplands where extreme day-time drought in summer is offset by nocturnal dew and mist. Here the animals often occupied separate summer and winter ranges (up to 120km apart). They moved between pastures and water sources on well-worn traditional paths. Where grazing permits, individual herds are seasonally residential (i.e. live within a 3–5km^2 range). Some local populations are less water-dependent than others; most prefer to drink daily and can dig into river beds with their hooves.

Cape Mountain Zebra
E. z. zebra

Below: Hartmann's Mountain Zebra, adult male and juvenile

FOOD Almost exclusively grazers (but will browse acacias on occasion). Grasses tend to be either patchy or sparse throughout their range (except for seasonal desert flushes). Recorded preferences are for *Themeda*, *Heteropogon*, *Cymbopogon* and *Aristida* species. *Stipagrostis* and *Hyparhennia* are other common grasses growing on deeply drained sites. Both individual grazers and social units tend to disperse more widely under these conditions. (They may also be less constrained by large carnivores, which are generally rare in such habitats.) The timing and intensity of grazing is strongly influenced by temperature and season, with animals taking shelter and becoming inactive during the middle of the day in summer.

BEHAVIOUR Breeding-age females are coerced by the largest, most active males into 'harems' of several mothers accompanied by their latest offspring. Such harem groups average five animals and seldom exceed 12. Both harem structure and home-ranges can become very stable and enduring. Elsewhere harems may be less permanent and highly mobile, with long daily or seasonal movements. Aggregations are temporary and seldom exceed 30. They rarely associate with other grazers. Non-breeding males, and occasionally young females, form small, unstable 'bachelor' groups.

Mountain Zebras are less vocal than other zebras. Subordinate animals appease superiors with a high, whistling whinny. A two-phase barking bray, most often made by the male, both alerts and draws his harem together. When dominant males meet, they circle and strut broadside.

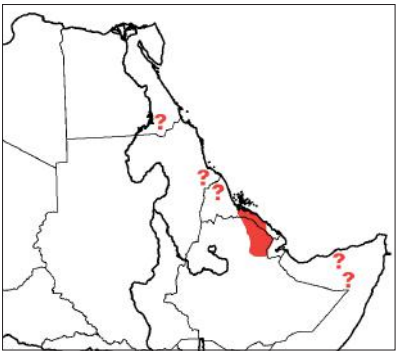
One foal is born after a 1-year gestation. The spacing of births varies. Nursing foals coerce their mothers to permit suckling by blocking her path and leaning against her chest. Most offspring have left or are chased out of the parental group by the time they are 2 years old. These zebras live for at least 25 years.

ADAPTATIONS The enlarged stripe pattern on the rump is visible from a greater distance than the vertical body stripes. This may help the zebras to maintain visual contact over wider distances on sparse grazing. The 'grid-iron' of smaller stripes above the root of the tail appears to be the target for 'chinning'. This is a form of ritual social behaviour in which the zebra (usually a male, but of any age) approaches another and presses the chin very forcefully on the 'grid-iron'. Actual grooming is very rare among adults but such rubbing, leaning and circling (especially among adult males)

may be accompanied by mouth-champing. This behaviour suggests an uneasy mix of social and anti-social impulses. Inhibited forms of nibble-grooming can be seen in the context of dampened aggression. The powerful optical stimuli involved in their encounters would appear to form part of a compelling socialising mechanism among adult Mountain Zebras.

STATUS The hunting of the Cape Mountain Zebra was officially prohibited in 1742 because it was already seen as rare and endangered at that time. However, the ban was ignored and the Cape Mountain Zebra was only saved from extinction by a single farmer, Henry Lombard, who kept 11 animals on his farm. There are now more than 1,390 in six reserves, all descended from the 1950 nadir of seven females. Hartmann's Mountain Zebra is at lower risk but populations suffer continued attrition as fenced ranches interrupt free movement and turn more and more grazing over to livestock. IUCN rates the species as vulnerable.

AFRICAN WILD ASS *Equus africanus*



African Wild Ass

OTHER NAMES Fr. *Ane sauvage*. Ger. *Wildesel*. Swah. *Punda*.

MEASUREMENTS HB (est.) 1.95–2.05m. T 400–450mm. Sh. ht 1.15–1.25m. W 270–280kg.

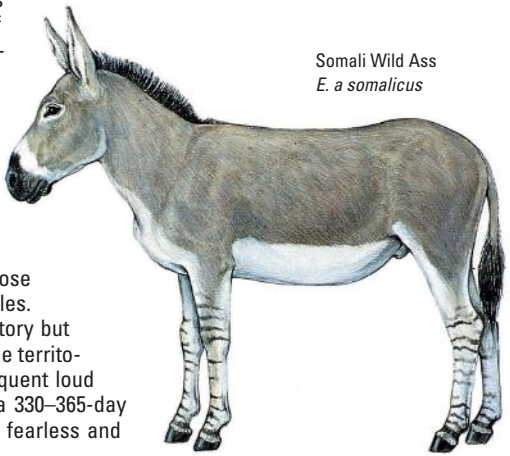
RECOGNITION The wild ancestor of domestic donkeys, the African Wild Ass is lean and muscular, fawn or grey, with a near-white belly and legs. It has a short, hairy black brush to the tail, a black mane and black margins to the long leaf-shaped ears. Hooves are exceptionally narrow.

GEOGRAPHIC VARIATION Nubian Wild Ass, *E. a. africanus*: grey with only the shoulder striped. Somali Wild Ass, *E. a. somalicus*: fawn, with only legs striped. Note: Algerian asses depicted in rock-paintings and Roman mosaics show a form with both leg stripes and at least one long, bold shoulder stripe. (Invalid NW African '*atlanticus*' identification was based on zebra bones!)

DISTRIBUTION Formerly Saharan region to Red Sea and Somalia (possibly in S Arabia in prehistoric times), in regions with a brief annual rainfall of 100–200mm. Now found in relict pockets on the Red Sea littoral, Danakil, Ogaden and Nogal valley.

HABITAT Semi-desert grasslands and dwarf shrublands (typified by aloes and euphorbias) where the asses tend to retreat into rocky hills and seek shade during the day. They are most active when the weather is cooler: at dusk, dawn and during the night. They are always within a 30km walk to water (but will tolerate brackish sources). They are able to go without water for about 3 days.

FOOD Grasses, notably *Eragrostis*, *Dactyloctenium* and *Chrysopogon*. Wild Asses are well adapted to graze the hardest of desert grasses, such as *Panicum* and *Lasiurus* species. They use their incisors and hooves to break open tussocks.


Somali Wild Ass
E. a somalicus

BEHAVIOUR Very small mother–offspring units are independent of each other but gather opportunistically in search of good grazing. Their preferred range is often within vast territories held by mature males. These may exceed 20km^2 and their boundaries with those of adjacent males are marked by dung piles. Other males are tolerated within the territory but all access to females is monopolised by the territory-holder. Oestrous females stimulate frequent loud braying in males. One foal is born after a 330–365-day gestation. Initially the foal is passive and fearless and

will remain alone for long periods while the mother seeks water to maintain her lactation. The foal can start grazing within weeks of birth but may suckle for as long as 6 months. Animals are known to live for 40 years in captivity.

ADAPTATIONS The small, narrow and very hard hooves of African Wild Asses are specifically adapted to firm and rocky ground. African Wild Asses avoid sandy areas and have always been absent from all the sandy dune regions of the Sahara.

STATUS African Wild Asses occupy the last vestiges of a formerly vast range. Intolerance by herders, degradation of the range by their livestock and poaching for meat, target practice or so-called 'medicines' have been the principal causes of their long decline. It seems their only immediate salvation lies in captive breeding (notably at Basle Zoo and Hai Bar reserve in the Negev Desert). Listed as endangered on Appendix I (CITES).

RHINOCEROSES RHINOCEROTIDAE

Black Rhinoceros	*Diceros bicornis*
White Rhinoceros	*Ceratotherium simum*

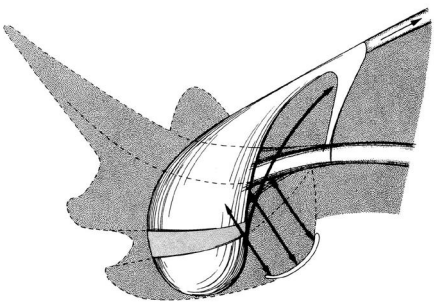
When animals have become as scarce as rhinoceroses have today it is difficult to describe them as successful. Yet living African rhinos were, until very recently, the widespread, abundant, advanced and successful representatives of a family that had seen a very wide range of types in the past (i.e. 30 fossil genera).

RECOGNITION Rhinos are the second largest land animals, only surpassed by elephants in bulk and weight. (An extinct rhinocerotid, *Paraceratherium*, with a shoulder height of nearly 6 metres, dwarfed elephants.) They have relatively short, powerfully muscled legs, a short neck and a massive head, armed with a nasal horn or horns. Contrary to popular belief, rhinos are not ponderous and slow but are capable of running or galloping fast. Their long, heavy bodies are densely bound masses of reinforced bone and muscle enclosed in very thick skin. Most of the rhino's great weight is taken on the broad central toe but two smaller hooved toes on each foot spread the load and enhance stability. Other characteristics include backward-facing genitalia that fire powerful horizontal squirts of urine. Males lack a scrotum and have undescended testes.

GENEALOGY The earliest rhinos were small, agile animals, something between a tapir and a horse in appearance. Large, horned forms originated in Asia. The first rhino immigration into Africa was about 20 mya; among the immigrants was a close relative of the living Sumatran Rhino (*Dicerorhinus*). This genus survived from at least 20 mya to less than 1 mya. Precursors of the two surviving African species first appear as fossils about 13.5 mya. The White Rhino appears to have split from a common ancestor with *Diceros* about 10 mya and has shown continuous adaptation towards grazing ever since. Both Black and White Rhinos are exclusive to Africa.

ECOLOGY The main rhino speciality is an ability to feed on coarse plant material. Rhinos are more selective than elephants but less so than most antelopes. Temperature control, digestion and scent communication all depend upon water, and rhinos are unable to survive extreme droughts. Nonetheless, rhinos formerly suffered very low levels of natural mortality, a trait that goes with long life (up to 50 years) and a slow breeding rate.

NATURAL HISTORY Rhinos display territorial behaviour yet can tolerate high densities and may even live in small herds. The tolerance of dominant individuals, particularly males, appears to vary by species, by region and in response to changes in density. Home-ranges are marked with dung and urine. Rhinoceros horns are solid keratin (like toenails or cows' horns). They are not set over a core but on a well-buttressed bone pediment that transfers all the stresses and strains of stabs, swipes and tosses to skull and forequarters (a rhino has been known to toss an adult horse into the air). Occasionally the rudiments of third or



Ceratotherium, principal mass of skull in relation to mastication, horns, vertebral column and suspension.

fourth horns may grow on the muzzle and forehead of rhinos and there was a tendency towards clusters of horns on the heads of various extinct species.

The teeth can withstand a long life of chewing on tough vegetation and are deeply embedded in bony mandibles. Their food is gathered in by very muscular lips. An envelope of thick, wrinkled skin partially disguises their magnificent heads. Rhino heads are almost architectural models of form and function. Enclosing the vital sense organs and articulated by huge jaw and neck muscles, the skull is reinforced against its own weight. Often dubbed 'prehistoric', rhinos are no more bizarre or 'primitive' than a pig or a cockerel and should be endowed with a future, not just a past.

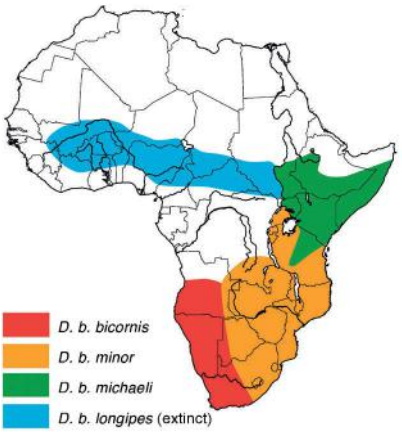
STATUS The extreme vulnerability of rhinos under genuinely wild conditions (due to the great price paid for their horns) has forced the vestiges into something close to domestication under armed guard. Rather than permit extinction to go ahead, it would seem sensible to accept that their survival now depends upon formal domestication, away from lawless areas. Until cultural and environmental attitudes have changed, rhino survival now depends upon captive or very closely managed populations. Unfortunately, in addition to poachers, pirates and rapacious markets outside Africa, the blinkered livestock industry is also a major obstacle to rhino survival.

BLACK RHINOCEROS *Diceros bicornis*

OTHER NAMES Hook-lipped Rhinoceros, Browse Rhinoceros. Fr. *Rhinocéros noir*. Ger. *Spitzmaulnashorn*. Swah. *Faru*.

MEASUREMENTS HB 2.90–3.75m. T 600–700mm. Sh. ht 1.37–1.80m. W 700–1,400kg.

RECOGNITION A very large mammal, its thickest skin forming inflexible plates over the shoulders, haunches, sides, forehead and cheeks. Skin around the muzzle, eyes, ears, undersides and legs is thinner and more flexible. The grey skin colour is most evident during the rains. Mud-wallowing and rolling in dust or ash discolours most hides during the dry season. Behind the shoulder, the dorsal silhouette swings down and back to raised haunches. The head has a short forehead and a very muscular, mobile mouth ending in a sharply pointed upper lip. The three toes leave characteristic tracks. Other signs of the Black Rhino's presence include rubbed trees, rocks and termitaries, well-scattered dung middens and habitually sprayed urine-posts.



former distribution of Black Rhinoceros subspecies (present distribution now highly fragmented)

GEOGRAPHIC VARIATION Black Rhinos were highly variable and over the years 23 subspecies were named. Some represented the conceits of trophy hunters, but others came from relict pockets where recent 'founder effects' had probably operated. Four regional populations correspond (very approximately) with four well-established subspecific names. *D. b. bicornis*, the largest form, was described from the Cape and has long been assumed extinct; however, surviving rhinos from arid Namibia are often allocated to this taxon, implying *D. b. bicornis* ranged well beyond the Cape. *D. b. minor*, a smaller-skulled type, ranged throughout SE Africa. *D. b. michaeli*, also small-skulled, occupied NE Africa. *D. b. longipes* ranged from Upper Guinea to the Nile but is now probably extinct.

DISTRIBUTION At one time Black Rhinos occupied a large part of sub-Saharan Africa in all but the wettest and driest areas (maximum dry-season range within 25km of water). Contemporary populations are on the brink of extinction and only hold out in a wide scatter of heavily guarded, minuscule pockets.

HABITAT These rhinos favour edges of thickets and savannas with areas of short woody regrowth and numerous shrubs and herbs. They are naturally scarce or absent in closed-canopy forests and woodlands and the more extensive areas of grassland. Where woody and leafy forage could support them, these rhinos were formerly found at very high densities (i.e. up to 23 animals, 17 wholly sedentary, in 2.6km^2). Where they were very common, smooth rhino pathways, dung piles, urine spray sites and rubbing posts were much in evidence.

FOOD Low-level browse (leaves, twigs and branches), typically in *Acacia*, thicket, hard-pan and riverine plant communities. Some 200 species from 50 families recorded. These rhinos have special

Black Rhinoceros
Below: Black Rhinoceros with upper lip extended

seasonal preferences for legumes and certain other plants are always avoided. Salt is a major attraction and their taste for salt is exploited by many tourist lodges. Animals can go for up to 5 days without water if their food is moist; otherwise they are always found within daily walking distance of water. Horns are occasionally used to loosen soil around roots or to break branches above the lips' reach.

BEHAVIOUR A female with her young is the basic social unit. Adult females may form temporary associations and animals that share a part or all of their range have an easy-going familiarity with one another instead of the aggression that is elicited by total strangers. Home-ranges can cover more than 130km^2, but some are as small as 2.6km^2. Overtly territorial behaviour is also very variable. Males in high-density areas are well acquainted with, and generally tolerant of, their neighbours (except in the presence of an oestrous female). Males in low-density areas meet less frequently and are more likely to be aggressive. Decline can be accelerated in an already thinned population because a few very aggressive males not only miss encounters with females in heat but their intolerance of other males further lessens the frequency of matings. Displays between males resemble those of stallions: there is much strutting, broadside with lowered head, flattened ears and rolling eyes. Various snorts during encounters seem to have different shades of meaning. The animals utter a series of snorts interspersed with pauses, and very loud grunts and screams punctuate serious fighting.

One young is born after a gestation of 15–16 months. It is soon mobile and begins browsing vegetation before it is 1 month old. It sucks milk for up to 1 year and only begins to drink water after 4 or 5 months. A mother generally drives off her previous offspring before a new birth and the interval between births ranges from 2 to 5 years. Both sexes are capable of reproduction at 4 or 5 years old but males can seldom compete with established males before the age of 10 years. In spite of a life spanning more than 40 years, this is one of the slowest recruitment rates of any large mammal.

ADAPTATIONS Although all-out frontal charges occur in high-intensity fighting, Black Rhinos tend to use their horns more like clubs or staves than rapiers. Mild jousting may be accompanied by shoulder-to-shoulder pushing and leaning. Weight and horn size are easily tested this way but scent and behaviour generally reveal the dominant individual. Avoidance or submission follow.

STATUS Human pride, superstition, greed and stupidity have combined to ensure astronomical prices for horns for conversion into dagger handles, cups, supposed medicines and aphrodisiacs. In 1900 some 600,000 Black Rhinos were thought to survive in Africa. By 1970 estimates had dropped to 65,000. By 2010 the total number of Black Rhinos living within 38 officially protected conservation areas (ranging in size from 62km^2 to 55,000km^2) was about 4,880. Weak responses to international piracy, centred in Somalia, means continued attrition of all rhino populations. The adoption of secure rhino farming as semi-livestock, notably in southern Africa (where more than 2,000 animals are breeding under rigorous protection), and perhaps outside Africa too, now seems their only hope. IUCN rates as critically endangered.

WHITE RHINOCEROS

Ceratotherium simum

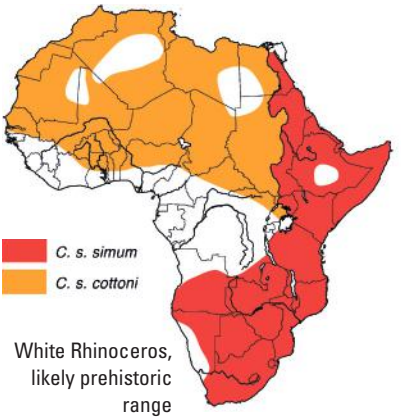
OTHER NAMES Square-lipped Rhinoceros, Grass Rhinoceros. Fr. *Rhinocéros blanc*. Ger. *Witrenoster*. Swah. *Kiaru ya majani*.

MEASUREMENTS HB 3.6–4.2m. T 800–1,000mm. Sh. ht 1.70–1.85m. W 1,400–2,000kg (♀), 2,000–3,600kg (♂).

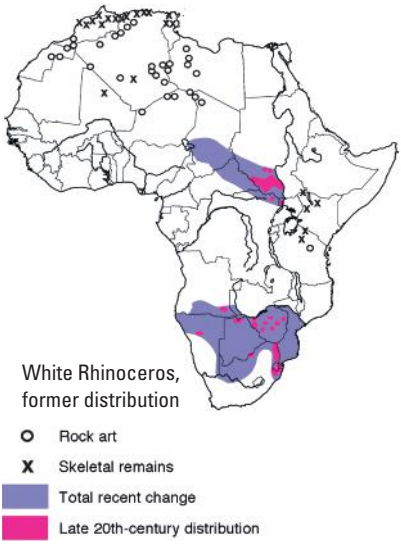
RECOGNITION Although called 'White', this very large rhino is of similar skin colour to the Black Rhino. The highest point behind the shoulder is mid-back (due to tall dorsal and lumbar vertebrae) rather than the haunches. The head is long (especially the forehead). The mouth is very wide, flat fronted and set low over the chin. The flexible neck forms a prominent hump when the head is raised. Spoor are more elongate than those of the Black Rhino, with greater separation of toes and a prominent cleft at the back.

GEOGRAPHIC VARIATION Southern White Rhino, *C. s. simum* (southern savannas); Northern White Rhino, *C. s. cottoni* (northern savannas).

DISTRIBUTION Fossils, bones and rock art suggest that this species was formerly abundant all over the better-watered grasslands of Africa (including much of the present Sahara). In historic times herds ranged around the shores of L. Chad but *C. simum* reached its nadir at the turn of this century with minuscule populations in two widely separated localities: Zululand and the DR Congo–Sudan–Uganda borderlands.



White Rhinoceros, likely prehistoric range



White Rhinoceros, former distribution

HABITAT A preference for short-grass areas and seasonal movements to avoid waterlogged long grass confirm that this species evolved within a larger ungulate community that maintained short swards. In areas of high density the rhinos themselves maintain grazing lawns. Where territories are maintained by resident bulls, their border-patrolling and scent-marking leave foot-scuffs, dung middens, urine sprays, rubbing posts and horned vegetation along boundaries. Linear pathways may form between grazing and waterpoints.

FOOD Short grasses, typically *Cynodon*, *Digitaria*, *Heteropogon* and *Chloris* species in well-trampled, well-drained, wet-season concentration areas, are preferred. After dry-season fires, White Rhinos may move into regrowth dominated by *Themeda*, *Hyparrhenia* and *Setaria*. Biting flies and direct sun may influence seasonal movements by restricting the rhinos to ridges or shaded areas for a time. Frequent alternation between grazing and resting changes to long midday rests at the height of the dry season.

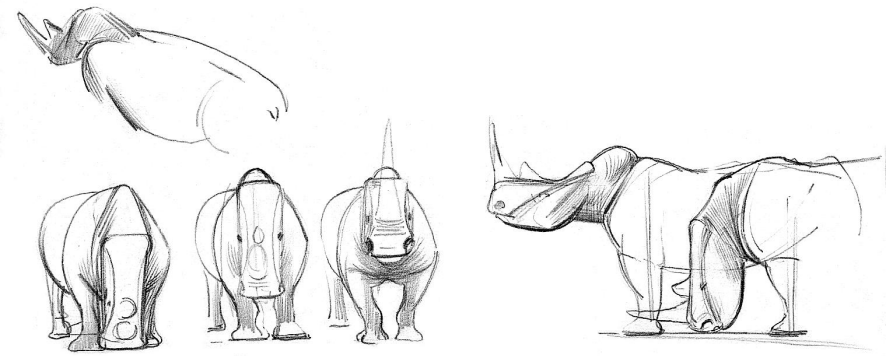
BEHAVIOUR Females and their immediate offspring occupy large (4–12km^2) overlapping home-ranges where they frequently graze alongside one or more female neighbours. Males defend territories but their size and their owners' tolerance is related to population density. In crowded Zululand parks male territories can be as small as 0.75–2.6km^2. White Rhinos are extremely vocal, with a wide repertoire of utterances. Infantile squeaks and pantings in adults become loud chirps, gasps and puffings (contact) or snarls and squeals of distress. Dominant males grunt and bellow challenges at other males or court females with a low, pulsing cry. One well-developed but hornless young is born after a 16-month gestation. It first grazes at about 2 months and is driven away by

White Rhinoceros

its mother at about 2–3 years of age. Females do not usually breed until they are about 5 years old, dropping their first calf at 6½–7 years of age.

ADAPTATIONS This species evolved from a common ancestor that was very similar to the living Black Rhino; modifications in the proportions of the mouth, skull and neck enabled it to become a more efficient, short-grass grazer. Thus the neck has become short but has to crank up a heavier, longer head. This is achieved by the tall vertebral spines, web of tendons and bunched muscles that give the animal its neck 'hump'. Broad, flat-edged lips enable short grass to be cropped efficiently. Long grass is grazed more clumsily.

STATUS After millennia of decline the southern form of the White Rhino was brought back from the brink of extinction through the efforts of one man, B. Vaughan-Kirby. From, perhaps, 20–50 animals in the earliest years of the 20th century, by 2010 the estimated population approached 20,200. The northern form was formerly more widespread and abundant, even numbering about 2,230 in 1960, but is now reduced to four captive animals. IUCN lists the northern form as critically endangered. The southern form is at lower risk but is still dependent on rigorous protection.



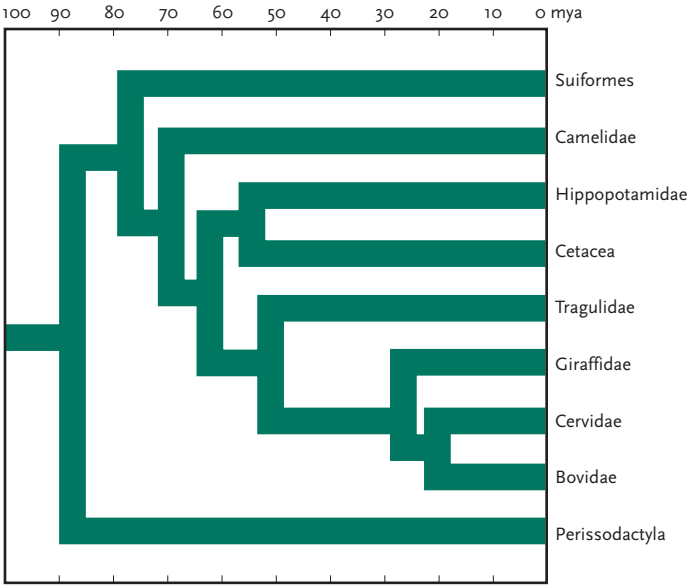
White Rhinoceros: grazing and head-lift behaviour.

The cetartiodactyls embrace all the horned antelopes and cattle, deer, giraffes, camels, chevrotains, pigs, hippopotamuses and, surprisingly, whales (which are not profiled in this guide). They are one of the most important and successful of mammal lineages. The earliest types were not very different from carnivores, had prominent canine teeth and an omnivorous diet. A very small, but significant shift in how body weight was carried distinguished the cetartiodactyl ancestor. Instead of body weight being taken through the central toe (as in perissodactyls), weight was distributed between the third and fourth digits. This probably enhanced stability on many soft or uneven substrates.

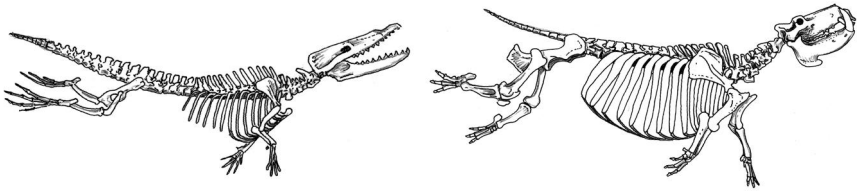
The most significant feature of this group is the progressive improvement of their digestion through a system of storing, re-chewing and sifting of the food and a symbiosis with bacteria and protozoans living within the chambers of the stomach. These break down cellulose and release nutrients. Notably Giraffes and hippos excel in digestive efficiency and economy

The skulls of living cetartiodactyls have been adapted to specific modes of combat requiring elaboration of canines, incisors, horns or antlers. Cetartiodactyls also show very diverse social and ecological adaptations.

The principal threat to African cetartiodactyls is their continuing replacement by a few exotic domesticates. An ever-expanding and aggressive livestock industry is eroding and exterminating natural communities of animals and plants on a huge scale, at inordinate cost to the long-term health of African environments.



Tentative phylogenetic tree for Cetartiodactyla (after Bininda-Emonds *et al.* 2007 and Hassanin *et al.* 2012).



Left: Skeleton of *Rhodocetus*, an early fossil whale (after Gingerich *et al.* 2001). *Right*: Skeleton of Common Hippopotamus.

PIGS SUIDAE

Wild Boar	*Sus scrofa*
Bushpig	*Potamochoerus larvatus*
Giant Forest Hog	*Hylochoerus meinertzhageni*
Warthogs	*Phacochoerus* (2 species)

RECOGNITION Pigs are robust, large-headed animals with relatively short legs and a compact body build. They have wedge-shaped skulls, out-turned canine tusks and a barrel-like snout that is tipped with a very tough, mobile disc mounted on a well-reinforced prenasal bone. All have leathery, sparsely haired skin. Weight is taken on the two central toes of each foot but the side hooves splay out in soft ground. The skulls of African pigs show striking adaptations to their preferred foods and to modes of tusk- or snout-fighting that are unique to each species.

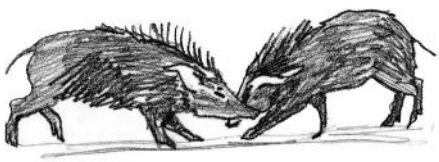
GENEALOGY Pig skulls are among the best preserved and most abundant of fossils in African deposits. Because morphological changes are rapid and reflect regional adaptation, they are excellent stratigraphic indicators. Originating in Asia about 30 mya, the ancestors of modern African species only appear about 4.6 mya in the form of *Kolpochoerus* from which first *Potamochoerus* and then *Hylochoerus* evolved within our continent. Warthogs have been thought to derive from *Metridiochoerus*, which entered Africa about 3.4 mya.

GEOGRAPHY An Old World group, pigs do best in moist areas with dense cover and soft soils, but the warthogs have adapted to arid Africa.

ECOLOGY Rootling is a primary adaptation in pigs. Wild Boar and bushpigs, the former in Eurasia and N Africa, the latter in Africa, are the most conservative in this respect. The bushpigs have branched into true forest and savanna-adapted species while the Giant Forest Hog has become a forest glade grazer. The warthogs have also become mainly grazers but have diverged into a mainline savanna species and a more specialised, arid-adapted form. The universal suid dependence on secure shelter or dens is met by self-dug or appropriated earth burrows.

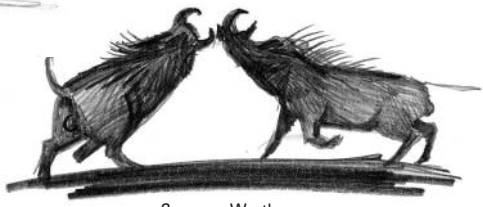
NATURAL HISTORY Social animals for the most part, pigs communicate mainly through scent and sound. They are highly vocal and well supplied with glands around the genitalia and mouth. Competition, especially among males, is very intense and has led to elaborate threat and appeasement behaviour. They have short gestation periods, large litters, fast maturation rates and very high mortality in the young.

ADAPTATIONS The primacy of scent and ability to dig with the nose disc is manifested in well-reinforced skulls with long, tubular muzzles. The disproportionately large head is used as a lever for food and as a weapon in trials of power and weight during contests. Short, sharp tusks are typical of primitive lateral fighters and 'snout-boxers' while more elaborate 'antler tusks' have been developed by warthogs. These species derive from ancient stock that included near hippo-sized animals.



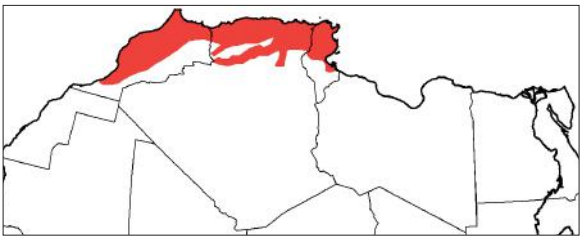
Bushpig

Giant Forest Hog



Common Warthog

WILD BOAR *Sus scrofa*



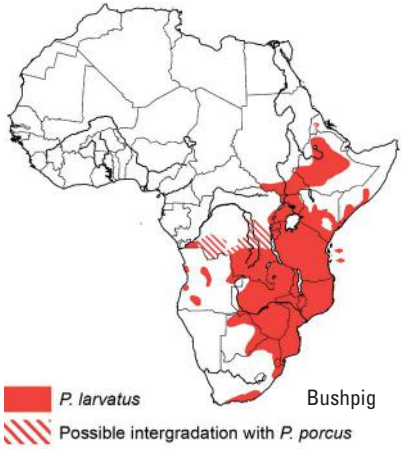
Wild Boar

OTHER NAMES Eurasian Wild Pig. Fr. *Sanglier*. Ger. *Wildschwein*. Swah. *Nguruwe mwitu*.
MEASUREMENTS HB 0.85–1.3m (♀), 1.0–1.6m (♂). T 150–210mm. Sh. ht 600–900mm. W 30–80kg (♀), 33–130kg (♂).
RECOGNITION A flat-sided and shaggy pig with a long snout, large, leaf-shaped ears and a short dorsal mane. Colour varies between dark grey-brown and a dirty tawny colour. Tracks reveal two oval hoof-marks (with side hooves only imprinting in mud).
GEOGRAPHIC VARIATION *S. s. algira* (often regarded as no more than a small, long-tusked variety of the European Wild Boar). Hybridises readily with bushpigs.
DISTRIBUTION Found over most of Eurasia. Originally the entire North African littoral but extinct in Egypt by 1902 and in Libya by 1890. Still occurs from the Atlas region to N Tunisia. In a feral state (derived from early domestic stock) in South Africa, Sudan, Pemba and Mafia and most recently introduced into Gabon and Burkina Faso.
HABITAT In North Africa mainly oakwoods and scrub; also in tamarisk groves on desert margins. Wild Boars make nests of gathered grass and branches or scrape a shallow depression in dense vegetation.
FOOD Omnivorous, with acorns the main seasonal staple in North Africa (at which time animals put on weight rapidly); also bulbs, roots, fallen fruits, snails, insect larvae and other invertebrates. Wild Boars occasionally scavenge and eat small vertebrates. The availability of food is the main determinant of their population cycles but climate, predation (in the past) and diseases such as hog cholera periodically kill large numbers of these pigs.
BEHAVIOUR Females and their young form associations with one or more other mother families. These have loose, temporary associations with adult males in the vicinity. The animals tend to be sedentary but are quick to respond to disturbance or hunting with rapid movement and changes in behaviour. Thus mainly diurnal habits can change to nocturnal habits and distances of 20–30km may be covered. Home-ranges are very variable, from 2–20km^2. Tusk glands, salivary secretions, genital scents and certain calls are all thought to facilitate courtship and mating. Three to 10 piglets are born after a gestation of 115 days. The mother gives birth in a nest of leaves, branches and grass, where she stays put for about a week before emerging, sometimes to rejoin other families in 'nursery groups'. The young grow rapidly and are sexually mature by about 1 year. They are annual breeders and have winter mating peaks. They live for up to 20 years in captivity, less in the wild.

ADAPTATIONS Wild Boar males are unique in having dense dermal shields of protective tissue under the skin of the shoulders and on the barrel of the chest. This limits the damage from lacerating blows suffered during frequent fights between males during the winter rut. The side-curving tusks are very sharp and are wielded with a very fast and powerful sideways swipe of the head.
STATUS Wild Boars fluctuate in numbers but are common and widespread in Morocco and Algeria where they are not eaten and seldom hunted. Their recent introduction into hunting reserves in Gabon and elsewhere is highly irresponsible.

BUSHPIG *Potamochoerus larvatus*

OTHER NAMES Fr. *Potamochère*. Ger. *Buschschwein*. Swah. *Nguruwe*.
MEASUREMENTS HB 1.00–1.77m. T 300–450mm. H 550–1,000mm. W 45–150kg.
RECOGNITION Compact, with a slab-like, short-legged body, tapering into the head and snout with little indication of a neck. Extremely variable in colour, it is always covered in coarse, shaggy hair. The dorsal crest and face are often white or grey. The body colour varies from blonde or red to grey, brown or black. Colour varies with sex, age, region or individual; as a result 17 subspecies have been named.
GEOGRAPHIC VARIATION Eastern Bushpig, *P. l. hassama* (uplands and eastern littoral); Southern Bushpig, *P. l. koiropotamus* (S and SE Africa). (Note: small pigs from the Horn of Africa have been called *P. l. somaliensis* but they appear to intergrade over a very broad front.)



DISTRIBUTION From the moister parts of southern Africa to the Congo R. and R. Kasai in the west. Likewise, the moister parts of East and NE Africa to the mountains of the central African Rift Valley. Bushpigs range up to 4,000m on Mt Kilimanjaro. They are thought to have been so recently introduced to Madagascar that early semi-domestication by Afro-Indonesian settlers on the mainland has been suggested as an explanation for their arrival on that island.
HABITAT A wide range of forested and woodland habitats, with a distinct preference for valley bottoms with dense vegetation and soft soils. Nest-making for raising young and in cold seasons is most prominent in the cooler parts of their range. More diurnal activity in the winter suggests that low temperatures are poorly tolerated.

FOOD Omnivorous and highly adaptive to local and seasonal conditions. Roots, tubers, bulbs and corms are the principal foods; also fallen fruits and herbage. In addition to fungi, Bushpigs take various animals, rooting for larvae and beetles, snails, amphibians and reptiles. They occasionally scavenge and a party has been seen to drive a Leopard off its kill. Seasonal changes in diet have been widely observed.
BEHAVIOUR A female and her young are often accompanied by an adult male within a restricted area where trunk-slashing along paths, rubbing posts and latrines suggest that males, and perhaps females too, are territorial, if only seasonally. Larger associations are seen

but only rarely. Home-ranges of up to 10km² have been estimated and nightly foraging walks of up to 6km. Contact grunts are common. Threats, assembly and alarm are all signalled by various grunts. Squeals and roars accompany fights in which contestants are sometimes lethally wounded or killed. Brow-to-brow pushing may be a preliminary to mating. Gestation (120 days) is followed by the female retiring into a nest or hollow to give birth to up to ten young. Piglets grow rapidly and slowly lose their brown and buff stripes over a period of months. They are sexually mature by about 18 months. Breeding is annual and seasonal, with most births at the end of the dry season (spring, i.e. September–November, in South Africa).

ADAPTATIONS Bushpigs occupy a wider range of habitats than the more specialised forest-dwelling Red River Hog. The relationship between these two species and the possibility of hybrid populations in Uganda and DR Congo await further study.

STATUS Bushpigs are a major pest for gardeners and farmers and are widely hunted for both control and meat. Without their natural predators they can become very abundant. They have been deliberately crossed with domestic pigs, and wild Bushpigs are reported to have hybridised with feral pigs in South Africa.

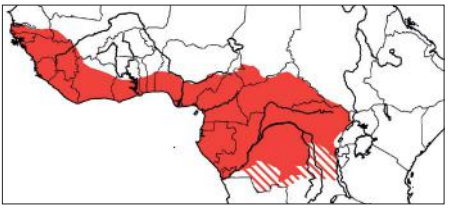
RED RIVER HOG

Potamochoerus porcus

OTHER NAMES Fr. *Potamochère*.
Ger. *Flusschschwein*.

MEASUREMENTS HB 1.00–1.45m. T 300–450mm. Sh. ht 550–800mm. W 45–115kg.

RECOGNITION A bright russet pig with a narrow white dorsal crest, white 'brows', cheek-tufts and jaw-line. The leaf-shaped ears end in a long white tassel. Muzzle and forehead are black and the fur is sleek and short over most of the body (except jaws and flanks which have longer hair).



Red River Hog

GEOGRAPHIC VARIATION Subject to differences and gradients in size; six named subspecies but these are generally judged invalid.

DISTRIBUTION The main rainforest belt from Gambia to E DR Congo and south to the Congo R./R. Kasai. Also in galleries wherever permanent water and soft soils are maintained in valley bottoms.

HABITAT Rarely outside rainforest, with a marked preference for river courses and swamp–forest margins. Here it ploughs up extensive areas while excavating roots and invertebrates. The narrow extent and linearity of its habitat in some areas may force semi-nomadic circuits of movement.

FOOD Omnivorous but with underground roots and tubers the main staple. Fallen fruits are of great importance locally and seasonally, as are invertebrates. Finding fruit supplies is assisted by the noise made by primates, hornbills and other fruit-eaters.

BEHAVIOUR Often found in small groups of up to 15 animals, the Red River Hog occasionally gathers in very large but temporary associations of up to 60 animals. During confrontations between males both animals strut broadside, with bristling fur and erect crests. They champ jaws, grunt, paw the soil and whip their slender tails back and forth. Champing clearly releases pheromones from the tusk and salivary glands while other secretions exude from the corners of the eyes, genitals and nape of the neck. Nothing is currently known of the nature of the information encoded in this

barrage of scents. Litters of very variable size are born, after a 4-month gestation, in a hollow tree or dense nest of gathered vegetation. For about 3 months the young are very prettily coloured in stripes of pale yellow and dark brown. At this time they crouch and 'play possum' when disturbed. As they age and their stripes fade, flight becomes the more normal response. Births have been recorded in February and March in Nigeria. Full grown at 2 years, captive specimens have lived for 20 years.

ADAPTATIONS Although the tusks of the male are short, they are very sharp and snout-boxing would tend to cut the large tendons and blood vessels that serve the rooting snout and its nostril disc. The Red River Hog has evolved knobbed, bony excrescences on the sides of the muzzle that appear to reduce the risk of such damage. The pocket behind this maxillary flange oozes a scented secretion. The facial pattern is well adapted for communicating contrasting signals relating to status. For example, horizontal ears signal aggression while vertically clamped ones indicate submission (see right).

Red River Hog, frontal head signals: aggressive (*above*), submissive (*below*)

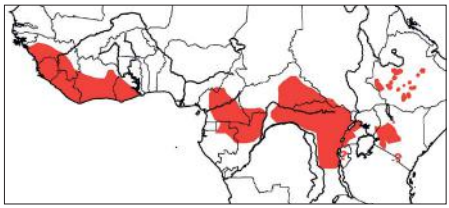
STATUS One of the staple species pursued by commercial bushmeat hunters. Although its fecundity allows it to keep up with this attrition in some areas, many rarer mammals are soon eliminated. Wherever forests have disappeared this species becomes scarce and it is now rare outside protected areas in the most westerly parts of its range.

GIANT FOREST HOG

Hylochoerus meinertzhageni

OTHER NAMES Fr. *Hylochère*. Ger. *Reisenwaldschwein*. Swah. *Senge, Nguruwe nyeusi*.

MEASUREMENTS HB 1.3–2.1m. T 250–450mm. Sh. ht 0.8–1.0m. W 100–200kg (♀), 140–275kg (♂).



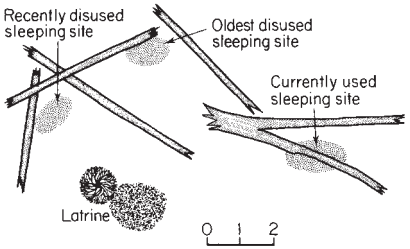
Giant Forest Hog

RECOGNITION Heavily built pig covered in long black hair. Mature males are about 50kg heavier than females and have enormous, naked cheeks, a broad, flat muzzle and thick tusks of moderate length. The rhinarium, or snout disc, may be more than 500mm across and is very broad and swollen. Over the forehead is a dish-like depression surrounded by a circle of raised bone, tissue and bare skin. Mature males also have grotesquely swollen preorbital glands, which can exude copious secretions that spread over the face. Very young piglets are brown- or straw-coloured, with side-striping most developed in the western parts of the range and mainly absent in the east.

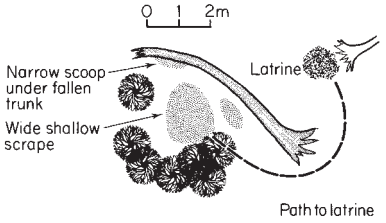
GEOGRAPHIC VARIATION Eastern Giant Forest Hog, *H. m. meinertzhageni* (east of Great Rift Valley); Congo Giant Forest Hog, *H. m. rimator* (W Nigeria to E DR Congo); Western Giant Forest Hog, *H. m. ivoriensis* (Upper Guinea).

DISTRIBUTION Scattered across tropical Africa in localised populations and in various vegetation types from sea level to 3,800m. They live in cold uplands as well as hot lowlands but do not tolerate low humidity or prolonged solar radiation. Their range resembles that of the Bongo antelope, which also exploits unstable forest-edge mosaics.

HABITAT Mainly forest/grassland mosaics but they range from subalpine areas and bamboo groves through montane to lowland and swamp forests, galleries, wooded savannas and post-cultivation thickets. A year-round and plentiful supply of green fodder and dense cover are found wherever these hogs occur. Their habitat is punctuated by sleeping sites, latrines, wallows, water holes, salt-licks and grazing meadows and is laced with a tracery of habitually used pathways.



Longterm sleeping sites in tangle of fallen timber



Frequently used sleeping site in dense forest

FOOD Many species of grasses, sedges and herbs, which are cropped at various stages of growth. In some montane areas herbaceous growth may also be very important. Giant Forest Hogs rootle very much less than other pigs and prefer to graze on mats of relatively short green grass. They masticate less thoroughly than warthogs (having lower-crowned molars) and differ in not selecting old or dry grasses. They seek salty earth which they excavate mainly using their lower incisors. After visits to salt-licks their dung may be mainly composed of earth. Latrines, usually sited very close to the temporary sleeping sites, are large and communally used.

BEHAVIOUR The basic social group is a mother and her offspring of up to three generations, but this unit may associate with a variety of neighbouring families. As sleeping-sites change frequently and are used by different permutations of neighbouring families, latrines may both advertise occupancy and help familiarise the changing sleeping partners with one another's scent. In Kenya the home-ranges of families probably comprise a series of overlapping foci but with each family having its own core area. In DR Congo males are thought to form more permanent bonds with particular families and core areas may have more of the character of defended territories. Males defend the females and young in their current family against other males and against predators (mainly Lions, Leopards and hyaenas).

They are often very vocal, using close-contact quiet grunts in thick cover and a louder barking call to establish contact over a distance. Males make an extended grunting call that builds up to a trumpeting crescendo and then dies away. Mating peaks are prominent but do not form a regular seasonal pattern in Kenya. In DR Congo mating peaks in March and in September, with births some 5 months later in August and February. Up to 11 piglets are born at a time and they remain in dense cover with their mother for about a week. The young are intensely playful and competitive, grow

rapidly and are weaned at 9 weeks and sexually mature by 18 months. In spite of very low survival rates, they can live for up to 18 years.

ADAPTATIONS Long sequences of fossil pigs that are immediate antecedents of *Hylochoerus* show that grazing was a relatively late development in this species. Grass-eating has involved the need for powerful lateral chewing. Developing the muscles and anchorage to support this has caused massive realignments in the skull and has led to unique forms of head-butting. The commonest contest, practised from an early age, is head-on snout-ramming. This form of contest is facilitated by the slightly bulbous, flat-fronted nasal disc which is not important for rootling. Most confrontations end in one male withdrawing but stalemate among larger, more evenly matched, mature males culminates in both backing off and charging from about 30m distance. When their massively reinforced foreheads meet in such clashes, the impact rocks one or the other back on its haunches. If the concave foreheads meet in exact opposition, a loud rifle-like report is produced by the escape of compressed air. Repeat charges may continue for up to 30 minutes with jaws champing, spittle flying and urine squirting every time. When the victorious male rejoins his group, preorbital secretions pour over his face, expressed from his grotesquely swollen glands. Submissive females gather to sniff him while adult males avoid him. Skulls are not infrequently broken but the 'false hull' structure of the skull (common to all pigs) protects the brain inside a well-insulated bony capsule. Broken skulls heal and their owners live to fight another day.

STATUS An easy target for hunters, especially those with dogs, which quickly bring them to bay, Giant Forest Hogs are threatened by commercial meat-hunting for urban markets. Unless such markets are prohibited it can be predicted that Giant Forest Hogs and many other species will disappear over most of their fragmented and declining range.

All populations are listed as rare and the most westerly ones (*H. m. ivoriensis*) as endangered (IUCN). They are nominally protected and are present in most forest parks and reserves within their ranges but are vulnerable even there because the grasslands and glades on which they depend are highly unstable. As a tractable grazing animal this species is a serious candidate for domestication or semi-domestication in equatorial Africa. Its potential needs investigation. Veterinary restrictions to protect domestic pigs from disease inhibit such initiatives and prohibit trade in any part of this animal.

WARTHOGS *Phacochoerus*

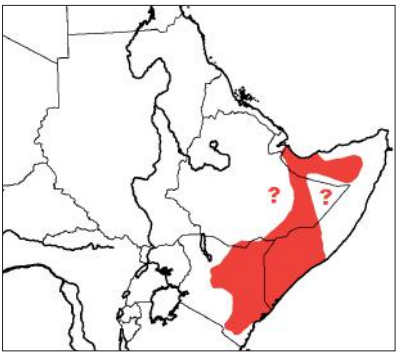
Survivors of a succession of now extinct African pigs, warthogs have become specialised grass eaters that have adapted their habits and diets to extreme seasonal and regional differences in grassland ecosystems.

Frontal views of Common Warthog (*left*) and Desert Warthog (*right*).

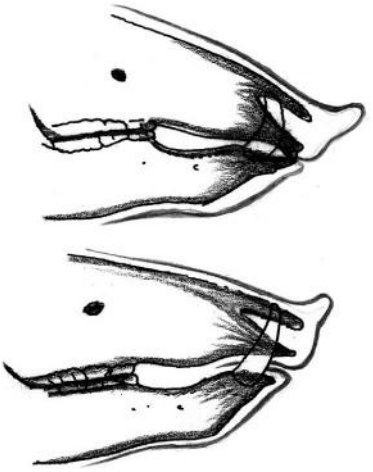
DESERT WARTHOG

Phacochoerus aethiopicus

OTHER NAMES Fr. *Phacochère du Cap.* Ger. *Desert Warzenschwein.* Swah. *Ngiri ya Somalia.*
MEASUREMENTS HB (est.) 1.0–1.5m. T (est.) 350–450mm. Sh. ht (est.) 500–750mm. W 45–100kg.
RECOGNITION Closely resembles the Common Warthog in size and general morphology but the dentition and the associated leverage for chewing have been modified and specialised, apparently towards more thorough mastication. The incisor teeth usually found at the front of both jaws are either totally absent or have become rudimentary and non-functional. The enlarged third molar is rootless and muscle attachments at the back of the palate are reorganised to allow greater lateral play. The head is relatively shorter and broader. The most obvious external differences are a more vertical snout, russet mane and 'droopy' sub-orbital warts.
GEOGRAPHIC VARIATION *P. a. aethiopicus* (Cape and Karoo): extinct. *P. a. delamerei* (Horn of Africa).
HABITAT The now widely separate subspecies are known from recent fossils outside their present range. They are so similar it is likely that an 'arid corridor' linked them, perhaps during the last Ice Age (20,000 years ago). The extinct Cape Warthog would have had to tolerate exceptionally cold and arid climates on the Karoo, conditions that were much more extensive during glacial periods. In modern Somalia this species survives under conditions that are drier than any currently tolerated by the Common Warthog. Physiological adaptations are therefore likely to distinguish the two species.
FOOD Desert Warthogs must graze and ingest excavated roots and rhizomes with their hard, sharp-edged lips. Common Warthogs only employ their incisors to wrench long tough grass or to



Desert Warthog

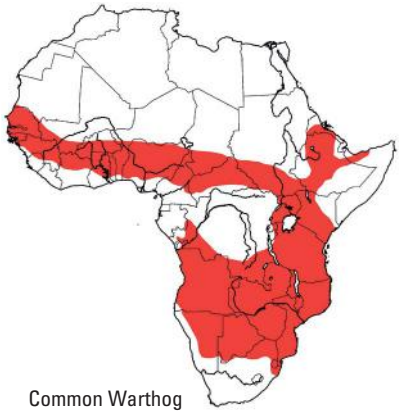


Above: Outlines of rhinarium (snout) and underlying nasal and mandibular occlusion in Common Warthog (*top*) and Desert Warthog (*above*).

excavate mineral-rich earth. Neither activity is possible for the Desert Warthog, which has possibly exchanged some minor dietary versatility for more thorough chewing and longer-lived molars.
STATUS After decimation by settlers and hunters in the Cape the remnant appears to have succumbed to the severe rinderpest epidemic of the 1890s. The Somali population is listed as vulnerable (IUCN). Its physiology and biology merit further study.

COMMON WARTHOG

Phacochoerus africanus


Common Warthog

OTHER NAMES Fr. *Phacochère*. Ger. *Warzenschwein*. Swah. *Ngiri, Mbango*.
MEASUREMENTS HB 1.05–1.52m. T 350–500mm. Sh. ht 550–850mm. W 45–75kg (♀), 60–150kg (♂).
RECOGNITION A relatively long-legged but short-necked pig with prominent, curved tusks. The nearly naked skin is grey. Lank black hair forms a dorsal crest that is longest over the neck and shoulders. Paler, often white bristles grow on the jaw-line callosity. The facial callosities, or 'warts', consist of three paired masses of thickened skin and connective tissue protecting the jaws, eyes and muzzle. Warthogs run at a high, jaunty trot, with back straight and the very narrow tail held vertically. The head, with its very protuberant eyes and ears, is held high. Feeding animals drop to their knees and commonly proceed to graze in this position, with their hindquarters raised.
GEOGRAPHIC VARIATION *P. a. africanus* (Senegal to Ethiopia), *P. a. aeliani* (Eritrea), *P. a. massaicus* (E and central Africa), *P. a. sundevallii* (SW to SE Africa).
DISTRIBUTION Common Warthogs are unusual pigs in that they are able to live in arid and open areas. In spite of greater tolerance of heat and drought, animals depend upon natural or self-dug shelters to escape extremes of heat and cold. They range up to 3,000m in Ethiopia and on Mt Kilimanjaro.
HABITAT Commonest on alluvial soils in lightly wooded country with a mosaic of vegetation types but well distributed throughout savanna and open-woodland areas of tropical Africa. High densities

are assisted by abundant Aardvark holes; deep burrows are essential to escape fluctuating temperatures and for protection from predators. Common Warthogs lack fur and surface fat and will insulate their burrows with grass, huddle together and bask in the sun to conserve heat.

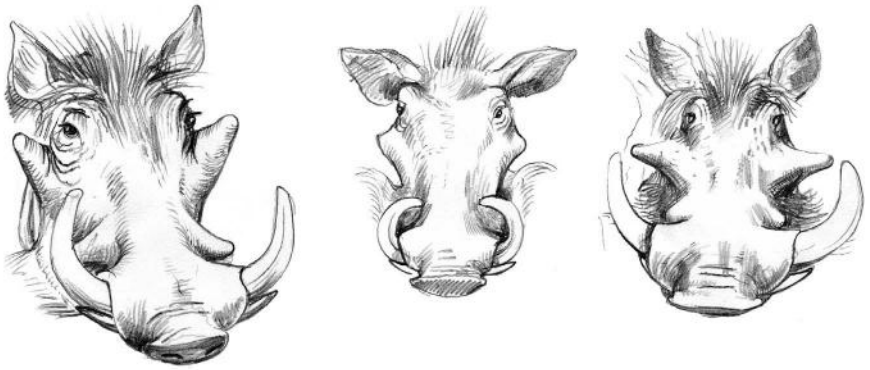
FOOD Grazing throughout the rains, Common Warthogs favour mats of short species, such as *Sporobolus*, *Cynodon*, *Panicum* and *Brachiaria*. They also strip growing grasses of their seedheads. In the dry season they turn to leaf bases and rhizomes that store nutrients over that period. They unearth these with the sharp edge of the nose disc. In Zimbabwe preferred rhizomes are from species of *Digitaria* and *Tristachys*. Common Warthogs occasionally eat fallen fruits, faeces and animal foods. Soil is regularly eaten, presumably for minerals. Although they generally stay within walking distance of water, these animals can subsist for a while on succulents and other water-conserving plants.

BEHAVIOUR There are several social levels. Mothers and their female offspring retain the most enduring bonds. Thus a new family unit joins others that are probably also close relatives. These loose groupings live within 'clan areas' averaging about 4km^2. Any one family occupies one-eighth to the whole of this area, circulating between favourite burrows that are well spaced out among 100 or more (any one of which may serve as a refuge). Any one hole is never exclusive to an individual or group, and families seldom share holes, simply avoiding occupied ones. The size of the families varies with the number and fortunes of offspring (litters average two or three but can number up to eight).

Young males remain with their mothers until driven off or associate together very loosely while they slowly reach full size. Male mortality can be high, and by the time adult males mature at 4 years they are solitary; as few as one survives for every four females. Mature males circulate among females and fights are probably in defence of mating rights rather than clan 'territory'. Courtship is initiated by the male when he finds an oestrous female. He pursues her, champing, salivating and mumbling in an engine-like 'chug, chug, chug'. The female slows her flight and eventually acquiesces. The young are born in a burrow after a gestation of 160–170 days. They grow rapidly, beginning to graze within 3 weeks, and can be weaned at between 2 and 6 months. Piglets squeak and churr and tend to run for the nearest burrow at any disturbance. Warthogs are known to live for up to 18 years.

ADAPTATIONS A grass and grass-root diet has involved many dental adaptations centring on the elaboration of a 'heel' on the back molar that has tripled its length. The last molars are long, very deep and durable. The rest of the tooth-row is more shallow-rooted and wears away. This contraction is linked with Common Warthogs having a more downwardly depressed muzzle compared to other pigs. They employ their tusks in 'tusk-wrestling' and pushing duels. Pushing is interrupted by lightning disengagements to thump at the side of each other's faces. Both deaths and fractures are frequent and it is the hammering that their heads can expect which has selected for the huge 'warts' (that play a role comparable to the pads worn for American football).

STATUS Common Warthogs have been eliminated from all intensively farmed areas, both as a nuisance and as a reservoir of livestock diseases. They are well represented in numerous national parks and are listed by IUCN as widespread and abundant.



Individual and sexual differences in the flare of tusks and the shape of the Common Warthog's warts.

WHIPPOMORPHA

A clade created to embrace both wh(ales) and (h)ippos. That the two might share a close common ancestry was never anticipated by morphologists nor by biology as a whole. Yet genetics have shown many dimensions to the relationship – similarities in milk proteins and limb structure as well as at the molecular level.

The shift from herbivorous to carnivorous diets took place after the whales' ancestor had become amphibious, which makes the hippo an appropriate analogue for the very earliest whale ancestors.

HIPPOPOTAMUSES HIPPOPOTAMIDAE

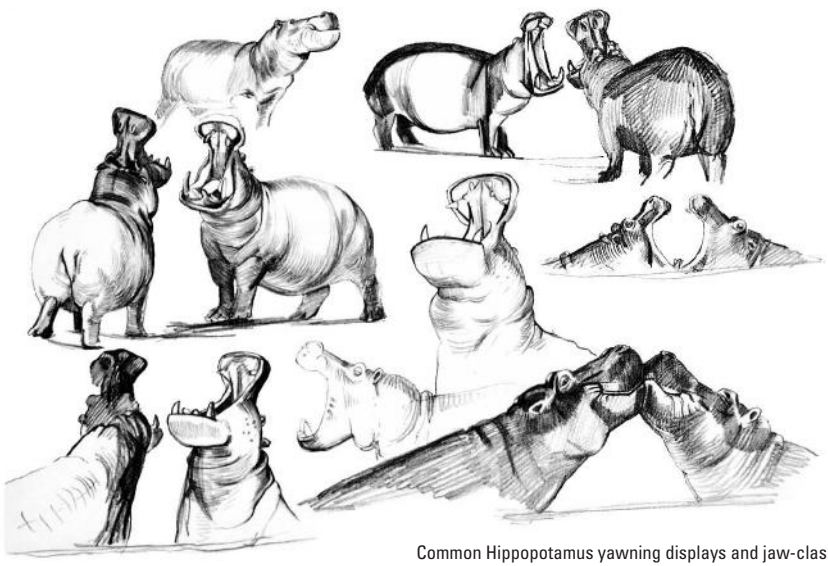
Common Hippopotamus	*Hippopotamus amphibus*
Pygmy Hippopotamus	*Choeropsis liberiensis*

RECOGNITION Hippos resemble gigantic, amphibious pigs with enlarged lower jaw and canines, four large, blunt toes on each foot and a very rotund body build. Their shiny, naked skin is densely perforated by minute skin-conditioning mucus glands.

GENEALOGY Hippos were once thought to have evolved from, or shared an immediate common ancestry with, pigs. Instead, hippos seem to have derived from a primitive extinct group named ancodonts. Other likely members were anthracotheres, fossils of which disappeared just as the earliest fossil hippos appear. The living pygmy hippo clearly represents a more conservative type. In many respects it appears to be more primitive than any known fossil. As recently as one million years ago there were at least eight species of hippo in Africa and four of these are known to have co-existed in the L. Turkana basin. These differed in size, diet and aquatic niche. Other hippos have disappeared from India and at least three species have disappeared in historical times from Madagascar.

GEOGRAPHY Hippos of different species survived in India until recent prehistoric times. The group's origins are probably African.

ECOLOGY Hippos' use of swamps and waters as day-time refuges has allowed them to develop a particularly successful ecological strategy. Great economies in energy are made possible by secure resting places, a slow but efficient digestion, a modest appetite for their size and broad, lawn-mowing lips that can gather enough food in a short period of the night.



Common Hippopotamus yawning displays and jaw-clashing.

NATURAL HISTORY Although hippos inhabit very secure refuges in swamps or water, these tend to be overcrowded and the focus for much competition and fighting, especially among males. Bulky animals fighting in mud or water engage one another's teeth, after which the contest largely becomes a trial of weight and strength.

Hippos have evolved a number of ingenious solutions to the problems of their amphibious existence. The young can suckle under water, through their hard, grass-cropping lips, by folding their extruded tongue around the nipple. Their need to disperse scent-marks has led to the evolution of a muscular, flat-bladed tail which turns like a fan or propeller to disperse the faeces.

ADAPTATIONS Among the most extensive modifications are a reorganisation of the skull and jaws to allow the lower mandible, its canines and incisors to take the brunt of fighting. This makes the lower jaw more massively reinforced than the upper. Its hinging is also organised to jackknife the skull upwards and transfer the main force of impact from the lower jaw almost directly back to the neck and shoulders. While the skin is well adapted to continuous immersion it also renders hippos vulnerable to dehydration. They cannot survive long away from water and only graze at night or during rain.

STATUS Both hippo species are serious candidates for domestication or semi-domestic ranching beside waterways and in association with pisciculture. However, current international fashions in animal husbandry present major obstacles to indigenising Africa's natural resources. No living domestic animal can compete with hippos for the economy with which they convert vegetation into animal protein. Both species have been eliminated over much of their former range.

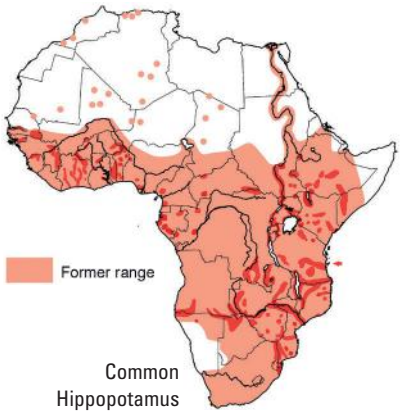
COMMON HIPPOPOTAMUS

Hippopotamus amphibius

OTHER NAMES Fr. *Hippopotame*. Ger. *Grossflusspferd*. Swah. *Kiboko*.

MEASUREMENTS HB 2.59–3.50m. T 350–500mm. Sh. ht 1.30–1.65m. W 995–1,850kg (♀), 955–2,065kg (♂).

RECOGNITION Common Hippos have stumpy legs and splayed toes that are just adequate for carrying their vast rotund body on land and fold neatly away while resting or swimming. Eyes, ears and nostrils have migrated to the top of the head in this species. The main colour of the smooth, shiny hide is a deep purplish-grey to blue-black. The underside, eye rims, ears and mouth show very variable expanses of pink. The hide is peppered with glands that exude a blood-like fluid that spreads to form a flexible varnish (antiseptic, sunburn cream, water-loss sealant and social perfume are among the suggested functions for this secretion). The sexes are strikingly different in proportions, males having larger canines and incisor teeth set in massive jaws and skull. They have a correspondingly huge jowl and greatly thickened neck.



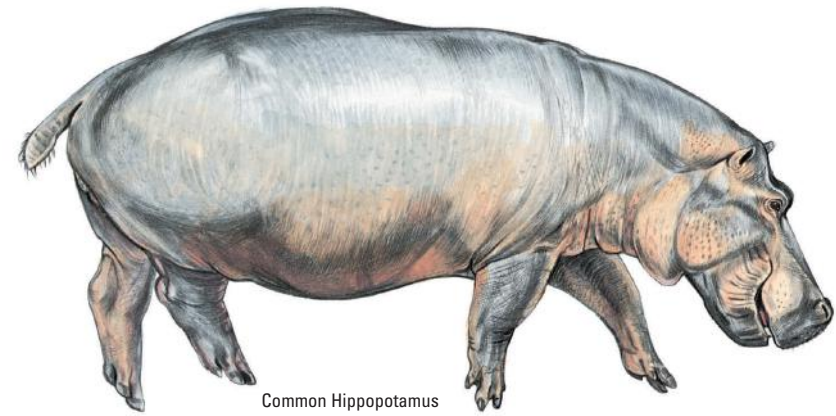
Common Hippopotamus

GEOGRAPHIC VARIATION Substantial regional variations in size but no subspecies recognised.

DISTRIBUTION Originally from the Nile delta to the Cape wherever the two requirements of permanent water and open grazing were met. Their upper altitude limit is about 2,000m. Present distribution is shrinking rapidly. Common Hippos aggregate in permanent water sources or wallows during the dry season and disperse very widely in the rains.

HABITAT A silent, solitary grazer on land by night, a vocal, densely social and sedentary wallower by day. The foreshore or bed of lakes and rivers influence Common Hippos, as does the depth and flow of water. Larger groups favour firm, gently sloping beaches and quiet waters, where they can stand or kneel on the bottom close to the surface. Large populations alter grass composition and inhibit fires by removing potential fuel. It is possible that such populations cause long-term vegetation cycles because their progressive degradation of the grazing increasingly encourages regeneration of thickets. Closely cropped lawns, paths radiating from the water and great accumulations of dung are characteristic signs of intensive use by Common Hippos.

FOOD Both creeping and tussock grasses are taken, notably *Cynodon* and *Panicum* species. *Brachiara*, *Themeda*, *Chloris* and *Setaria* are other important sources of grazing. The Common



Common Hippopotamus

Hippo crops grass entirely by means of its leathery (not muscular) lips. It walks slowly, closing its lips over mouthfuls of grass and wrenching them away with a regular swinging of the head. A Common Hippo can ingest up to 60kg in a night's grazing and seldom needs more than 5 hours out of the water. In Uganda, where pioneering studies of African ecology (and hippos) have taken place, fishermen and other villagers have been permitted to keep livestock inside national parks; as a consequence much disruption and erosion of Common Hippo habitat is taking place.

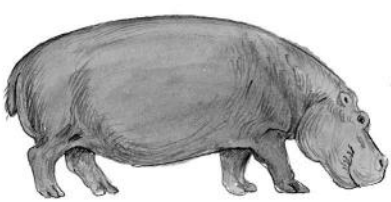
BEHAVIOUR Common Hippos have a very hierarchical society in which individuals must advertise their status and condition, especially to superiors. Voiding urine or dung, and prostration in the face of a dominant individual are normal modes of appeasement.

Females accompanied by up to four successive offspring are the only stable social unit. Individuals periodically change their resting sites but degrees of sedentariness or nomadism are highly variable. The largest males occupy narrow strips of water and land along the foreshore, the exact size of which can be quite variable. Here they defend exclusive mating rights but tolerate most subordinate males. Both female and bachelor associations are unstable in composition and vary a great deal in numbers. Aggregations range between 2 and 150.

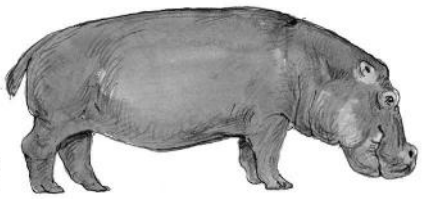
Large groups are very vocal, the main call being a reverberating nasal wheeze followed by a series of guttural honks. In the early morning this is associated with the return to water. It is the response to all disturbances, particularly in the evenings as the hippos begin to move. Males also wheeze-honk while copulating (the female lies prostrate).

One young (very rarely two) is born after an 8-month gestation. The mother segregates herself for up to 2 weeks after a birth, during which time she is very alert and aggressive. The young begins to graze after some weeks but is suckled for 8 months or more. Calves are quite playful

Distribution of Common Hippopotamus groups along a stretch of the Nile (after Laws *et al.* 1975).



Common Hippopotamus, female

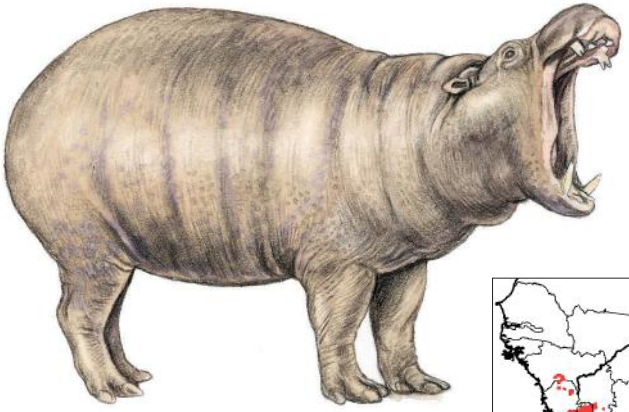


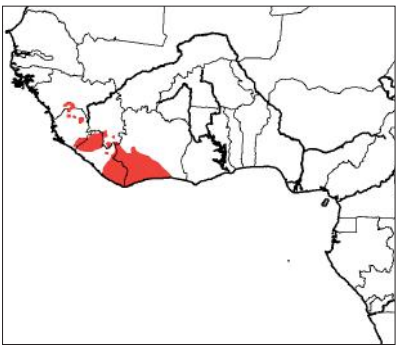
Common Hippopotamus, male

during this period. They continue to grow over 5 or 6 years and females become sexually mature between 7 and 15 years of age (males rather younger but they tend to be excluded from breeding for much longer by heavy dominant males). Births are spaced at about 2-year intervals. Common Hippos can live for up to 50 years in captivity, but probably do not survive as long in the wild.

ADAPTATIONS The body size and weight of adult females tends to stabilise at a regional norm, but males continue to grow, albeit very slowly, throughout life. This favours the oldest, heaviest males in their efforts to monopolise mating. A willingness to fight is advertised by yawning displays that are unique to the Common Hippo and contests are settled by clashing lower jaws together (which leads to much chipping of teeth). The incisors are modified to act like the antler tines of deer, allowing contestants to parry or get a purchase for a pushing contest. It is with the pushing contest that weight and jaw span are decisive. Younger males actively seek contests with frequent yawn displays that are preceded by a scooping up and violent tossing of waterweeds. Such rituals may be drawn out to last an hour or more, jaw to jaw, with occasional straining and weight-testing.

STATUS In spite of an extensive overall range, Common Hippos are very vulnerable to determined hunting. They are well represented in many national parks but suffer continuing local extinction. They are mainly hunted for their meat and in retaliation for the damage they cause to unfenced agriculture. They are readily re-introduced and can be controlled with fences and ditches. They have outstanding potential for domestication or ranching and make popular zoo exhibits.





Pygmy Hippopotamus

PYGMY HIPPOPOTAMUS

Choeropsis liberiensis

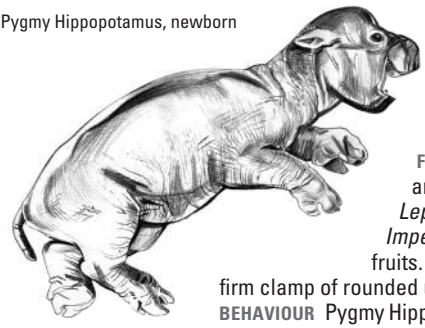
OTHER NAMES Fr. *Hippopotame nain*. Ger. *Zwergflusspferd*.

MEASUREMENTS HB 1.42–1.77m. T 150–210mm. Sh. ht 700–920mm. W 179–273kg (sexes are of similar size).

RECOGNITION Rotund-bodied, thick-necked hippo with a similar rounded, toothy muzzle (but proportionately much smaller head) to the Common Hippo. Eyes, ears and nostrils do not protrude as much as in the Common Hippo. The body is naked, sepia-brown with lighter, more fleshy colouring on the throat and belly. The thin, sun-sensitive skin resembles that of the Common Hippo in its physiology and the secretions that give the animal's entire surface a glossy sheen. The toes, less webbed and more widely splayed than those of the Common Hippo, leave a distinctive 4-pronged spoor.

GEOGRAPHIC VARIATION *H. l. liberiensis* (Upper Guinea), *H. l. heslopi* (R. Niger and R. Cross deltas).

DISTRIBUTION In geologically recent times very similar species occurred in India, Madagascar, S Europe and E Africa. Until recently the African population has been divided into two separate populations. The western population is now fragmented into minuscule relicts, restricted to forests between the R. Corubal and R. Bandama. The Cross R. and R. Niger delta populations are now considered extinct.


Pygmy Hippopotamus, newborn

HABITAT Pygmy Hippos inhabit forested watercourses, where they shelter by day in ponds, rivers and swamps. At night they follow tunnel-like paths through dense riverine vegetation to graze in glades, clearings, chablis or along grassy margins of swamps and trails.

FOOD Graze consists of various green grasses and herbs, notably the main broad-leaf forest type, *Leptaspis*, species of *Andropogon*, *Hyparrhenia* and *Imperata*, various sedges, herbaceous shoots and fallen fruits. Food is cropped by tearing the plant between the firm clamp of rounded upper and shovel-shaped lower lips.

BEHAVIOUR Pygmy Hippos have only been recorded singly, in twos or, rarely, a mother and her offspring in temporary association with a male. They are normally very silent but captive specimens have been recorded snorting, grunting, squeaking and hissing. They also make a much quieter groaning equivalent of the Common Hippo's honking call. They bear one young after a 6–7-month gestation. The young is guarded by its mother who suckles it for up to 6 months, during which time it grows rapidly. The mother may have a second calf after 2 years, at which time previous young are likely to be repelled. The young are feeding on vegetation by 3 months and mature by 3 years. Captive specimens have lived for 30 years.

STATUS In spite of formal protection since 1933, Pygmy Hippos have declined drastically. This is partly due to extensive deforestation and to hunting. Although there are currently 350 animals held in 131 collections, they are mainly kept as pairs or singles for 'display' and mortality is high. Captive breeding is probably the only realistic hope for their survival in the short term because few, if any, of the relict populations are adequately protected. The Nigerian subspecies is critically endangered. IUCN rates the species as endangered.

RUMINANTS RUMINANTIA

In its contemporary meaning, Ruminantia describes and embraces most, but not all, two-toed herbivores and it subdivides into two main divisions (infraorders) that are based on the detailed structure of the stomach. One, the Tragulina, (or Traguloidea, sometimes described as Proto-Ruminants) lack an omasum, one of the sacculations of the stomach (thought to act as a sieve to hold back larger plant particles). The other division, Pecora, or 'true ruminants' comprises giraffes and two parallel lineages, deer and bovids. Both have made independent radiations to fill equivalent niches, one mainly in the northern hemisphere, the other with its greatest diversity among African antelopes.

CHEVROTAINS TRAGULIDAE

Chevrotains are small, spotted ungulates that superficially resemble duikers. They are the last relic of a family that diverged from the pecora some 51 mya and was widespread in the Old World from 40 to 25 million years ago. They share some features with pigs but, unlike them, have remained relatively generalised. The more recent evolution of bovids is thought to have preempted many or most avenues of specialisation. However, chevrotains had a head-start in adapting to the heavily shaded floor of equatorial forests. This appears to have favoured a versatile animal with a varied diet, living a solitary life at low densities.

Details of chevrotain anatomy, physiology and behaviour illuminate the progress of evolution, especially by illustrating early essays in ruminant existence.

There are other species of chevrotain in Asia, where the smallest are known as 'mouse-deer'.

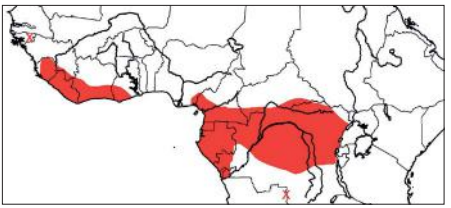
WATER CHEVROTAIN *Hyemoschus aquaticus*

OTHER NAMES Fr. *Chevrotain aquatique*. Ger. *Hirschferkel*.

MEASUREMENTS HB 620–1,020mm. T 75–150mm. Sh. ht 300–400mm. W 7–16kg (av. 9.7kg ♂, 12kg ♀).

RECOGNITION A compactly built ungulate with a short, thick neck, small, narrow head, leathery nose, slit nostrils, canine tusks and inconspicuous ears. The hindquarters are powerfully muscled

but the lower limbs are short and delicate in relation to the length and bulk of the body. The feet resemble miniature pig's trotters; they have naked, shiny black skin behind the hocks. The sleek, reddish-brown coat is marked with longitudinal white stripes on the sides interspersed with bold dorsal spots. The throat and chin are covered in coarse hair boldly patterned in black and white. This coarse hair may act as a dispenser for scent secreted by chin glands unique to the chevrotains. When the tail is raised (or 'flashed') it reveals a vivid white underside.



Water Chevrotain

Water Chevrotain

GEOGRAPHIC VARIATION Three subspecies are named but not considered valid.

DISTRIBUTION From Guinea to W Uganda in well-watered equatorial lowlands.

HABITAT River valleys within lowland rainforest, the margins of swamps or streams. Never outside dense cover by day, it may forage in exposed clearings, floodplains, open riverbanks or sandy flats at night. It is reported to clamber into tangles of vegetation and up sloping tree trunks (perhaps to sunbathe). Water is a major refuge from predators but only for brief periods. Animals can dive and progress under water but quickly tire. Diving is a last resort after 'freezing', often in a shallow form or concealed refuge. Hollow trees or underground burrows may also be used during the day.

FOOD Mainly fallen fruits, notably figs (*Ficus*), *Pseudospondias*, palm nuts (*Elaeis*) and breadfruit (*Treculia*); also the fruits of gingers, arrowroots and many others. Insects, crabs, scavenged meat and fish have also been recorded. The Water Chevrotain relies mainly on scent in order to find food. Chemically protected plants that deter other herbivores are taken and the chevrotain digestive system is physiologically adapted to detoxify a wide range of plants.

BEHAVIOUR The social system resembles that of a solitary carnivore. Females are spaced out in isolated home-ranges with minimal overlap or contact. Related females occasionally share a range but without much contact. Male ranges overlap those of at least two females. Young males cluster around what are probably parental ranges but frequent wounding suggests that male competition, enforced with long, sabre-sharp canines, helps space out fully mature males so that they are up to several kilometres apart. Combatants rush forward with mouths wide open and make lateral swipes with their canines. Males are more aggressive and active than the larger females. When females fight (they possess shorter, blunter canines), they utter a high, pulsing chatter. They scream when wounded and bark in alarm. Weak bleats may be rare contact calls.

When a female is in oestrous the male follows, calling through closed mouth. At each cry the female stops, as if by reflex, whereupon the male licks her rump. After many repetitions she permits copulation. One young is born after a 4-month gestation. Females are reputed to defend their offspring. The young lie up and are relatively inactive during the first 3 months, nourished almost entirely on milk sucked during periodic visits by the mother. Weaning coincides with dispersal at 9 months, about the time of sexual maturity, although full size and full dentition is only reached at 2 years. Although few survive 8 years, Water Chevrotains are estimated to live for up to 13 years.

ADAPTATIONS Both rump and throat are well protected in both sexes by a dense, thick skin and deep dermal muscles. These undoubtedly mitigate the severe wounds inflicted by the males' sharp canines.

STATUS Naturally sparse and widely spaced, this species is known to suffer intensive hunting and has become rare in many parts of its range. It is also known to be susceptible to disturbance and animals leaving formerly well-known areas are unlikely to live long away from them. Their survival depends upon the continued existence of substantial areas of undisturbed primary and old secondary forest.

GIRAFFES GIRAFFIDAE

Giraffe	*Giraffa (camelopardalis)*
Okapi	*Okapia johnstoni*

RECOGNITION The two surviving giraffes are both tall, browsing animals whose long muscular tongue has been modified to serve as a plucking organ. They have 'horns' that begin as cartilaginous buds in the skin of the forehead. These become bony and eventually fuse to the skull below. Horns are covered throughout life with skin and fur. In males bone continues to build up over the horns, orbits, nape and nose. Eventually the cap of rugose bone and thickened skin dwarfs the features below. Both the Giraffe and the Okapi have tall shoulders and sloping hindquarters.

GENEALOGY Ancestral giraffes may represent one of the earliest cetartiodactyls to combine a shift out of the forest with enlarged body size. Thought to have derived from a long-legged, almost two-toed chevrotain-like ancestor about 24 mya, they diversified into many species, some becoming extinct quite recently. They included a grazing okapi (*Samotherium boissieri*), the giant-antlered *Sivatherium* and *Libytherium*. Recognisably true giraffes were the tall, heavy *Giraffa jumae* and the lightly built *G. gracilis*. Giraffes were widespread and diverse in Africa and S Eurasia between about 15 mya and 1 mya.

ECOLOGY Giraffes select very high-quality foliage and, in spite of being cud-chewing ruminants, rely less on mastication to release nutrients than on digestive efficiency. They have very large, tough, tongue-like papillae in the stomach which provide the largest absorptive surface area known in any ruminant. This very efficient stomach is half the size of that of a grass-eating African Buffalo. Long-necked Giraffes flourish where there is abundant, year-long browse above 2m and below 5.5m. Not only are they clumsy at lower levels but competition from antelopes makes low-level herbage a mere emergency food. The Okapi exploits a lower, narrower browsing zone but its forest competitors are shorter still in stature and fewer in number.

NATURAL HISTORY Female giraffes are both shorter and more lightly built than males and feed from a narrower stratum. To compensate, they eat a wider variety of food species over a larger area. Further specialisations of this sort may explain how several giraffe species could co-exist in the past.

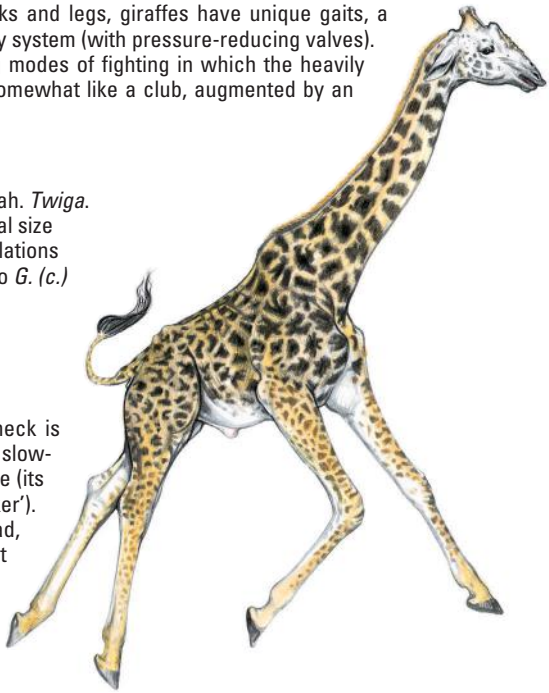
ADAPTATIONS Apart from their long necks and legs, giraffes have unique gaits, a unique digestion and a unique circulatory system (with pressure-reducing valves). They also have unique shoulder-leaning modes of fighting in which the heavily reinforced, blunt-horned head is used somewhat like a club, augmented by an occasional kick.

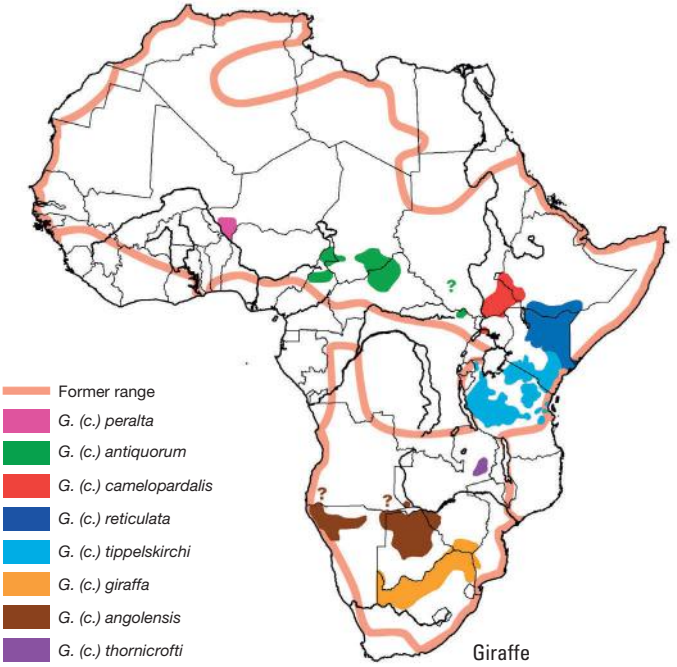
GIRAFFE *Giraffa (camelopardalis)*

OTHER NAMES Fr. *Girafe*. Ger. *Giraffe*. Swah. *Twiga*.

MEASUREMENTS Note that very substantial size differences exist between different populations and that the most reliable records refer to *G. (c.) giraffa*.
Total height 3.5–4.7m (♀), 3.9–5.2 (6.6?) m (♂). Sh. ht 2.72–2.92m (♀), 3.13–3.47m (♂). T 760–1,100mm. W 703–1,049kg (♀), 972–1,511(1,930?)kg (♂).

RECOGNITION The length of a Giraffe's neck is matched only by that of its legs, and its slow-motion lope covers ground at a great rate (its Arabic-derived name means 'fast walker'). The legs end in enlarged hocks and broad, rounded hooves. Giraffes can run at 60kph, at which rate the hoof may pivot forward so that the animal's weight is borne directly on the hock. Both young and old are able to outstrip





Giraffe

most predators. The neck is fringed with a short, thick mane and both sexes develop 'horns' above the eyes. Bony protuberances above the eyes preclude the Giraffe from being able to see upward. The face is strongly tapered and a 450mm tongue is the principal means of gathering foliage in to the large, elastic mouth and lips.

Given the familiarity of Giraffes in zoos and parks and their images in media, biologists, like most of the public, generally thought of the Giraffe as a single species. Two major genetic studies have challenged this assumption and demanded a re-assessment of Giraffe taxonomy and nomenclature. A major conclusion to emerge has been recognition that Giraffes from the centre–west realm have been genetically separate from Giraffes in the south–east realm for some 1.5 million years. Excepting small Reticulated Giraffes from the Horn of Africa (which probably deserve to be treated as a third major population), subpopulations within each of these realms are much younger.

Because no known fossils of modern Giraffes pre-date the Pleistocene, it is likely that the Giraffes' common ancestral population began to diverge not long after its initial spread through all African savannas. When populations, such as those of Giraffes, are more distinctive genetically than their appearance and anatomy suggests, grouping species into a super-species offers a useful naming system and that course is followed in this revised edition. While the two or three geographic mega-units (centre–west, south–east and Horn of Africa) clearly exist at a higher level of distinctness than do the regional subpopulations, the Giraffe species-groups presented here follow precedent in accepting a total of eight members. Colours vary greatly between individuals and occasional 'sports' have bizarre patterns, from uniform fawn or black to various blotchy permutations. In spite of this variation, all the populations listed below are morphologically distinct. The ranges cited here are historic because most Giraffe distributions are now vestigial.

Centre–west realm

West African Giraffe, *G. (c.) peralta* (includes *renatae*): W of L. Chad to Senegal.

Kordofan Giraffe, *G. (c.) antiquorum* (includes *congoensis*): W of R. Nile to L. Chad between 2° N and 14° N.

Nubian Giraffe, *Giraffa (c.) camelopardalis* (includes *rothschildi* and *cottoni*): E of R. Nile and W of Ethiopian dome, from Equator to 16° N.

Horn of Africa arid focus

Reticulated Giraffe, *Giraffa (c.) reticulata*: Horn of Africa E of Ethiopian dome to R. Tana. Thought to hybridise with Masai Giraffe between R. Tana and R. Galana. Also to hybridise with Nubian Giraffe along the Lorogi plateau to Samburu Hills (possibly further west too).

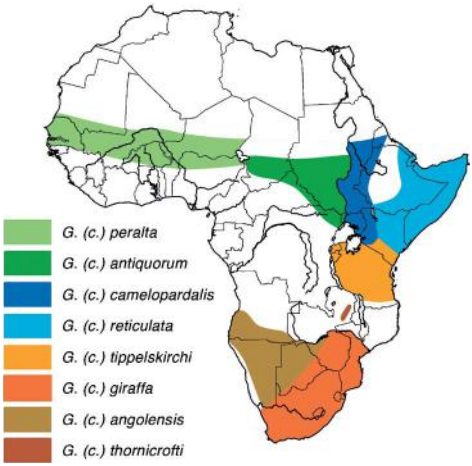
South–east realm

Masai Giraffe, *Giraffa (c.) tippelskirchi* (includes *schillingsi*). Tanzania and S Kenya from Galana R. south to Rufiji R. Thought to hybridise with *reticulata* between R. Galana and R. Tana.

Cape Giraffe, *G. (c.) giraffa*: southern Africa.

Angola Giraffe, *G. (c.) angolensis*: Kalahari and neighbouring *Acacia* country in SW Africa.

Luangwa Giraffe, *G. (c.) thornicrofti*: isolate in Luangwa valley.



Historic Giraffe ranges interpreted as three major populations with mixed or intermediate types along boundaries.

On present genetic evidence the eight forms listed above are claimed to be discrete, with each population behaving like an isolated species. In at least one instance where the range of a long-established regional population abuts that of its neighbour (the 'Galana hybrid zone' between *reticulata* and *tippelskirchi*) many observers have pointed out that most individual Galana Giraffes exhibit permutations of coat pattern that strongly suggest widespread hybridisation (one example is pictured here). Other apparent overlap zones have been suggested in the past but, with all ranges shrunk and so many Giraffe populations facing extermination, the argument may never be settled.

DISTRIBUTION Formerly widespread throughout the drier savannas of Africa (including the Sahara and Atlas Mts during the wetter conditions of about 7,000 years ago). They range up to 2,000m but are rare in precipitous hilly country.

HABITAT Present situations are a poor guide because most Giraffe habitats are now under agriculture. They remain mostly in savannas, open woodlands and seasonal floodplains (with abundant raised, thicketed termitary islets). Commonest in areas where rainfall, soils, wind, fire, elephants or flooding favour scattered low and medium-height woody growth. They are especially associated with savannas where *Acacia*, *Commiphora* and *Terminalia* are abundant trees.

FOOD Known to feed from more than 100 species of plant but *Acacia*, *Commiphora* and *Terminalia* species are major staples. Feeding and movement patterns differ from wet to dry seasons. The wet season is a period of abundant, green deciduous growth, during which time the Giraffes are widely dispersed. During the dry season they concentrate where evergreens survive. Sustained pruning of scattered bushes maintains a sort of acacia lawn. Irregular firing forces medium-term rotations by burning off light twig growth and removing browse for one or more years.

Giraffes, their extinct relatives and other browsers are thought to have shaped the biology of their food trees, including the evolution of thorns and galls, and the growth form of branches. Persistent and heavy browsing not only shapes the trees' form but can either delay or stimulate further growth.

The amount that Giraffes eat in a day varies but is less than half the intake of typical grazers. It is the concentrated nutritional value of the foliage they select and super-efficient digestion that makes modest feeding possible.

BEHAVIOUR All social units are temporary. Adult male Giraffes may be vestigially territorial because mature bulls monopolise all matings and tend to be intolerant of other large males at the cores of their very variably sized home-ranges (cores may be as large as 80km^2 but year-long movements are known to range from 5 to 654km^2 or more). Females have very unstable home ranges that may drift from year to year. These overlap those of very many other females, with which they may associate (in mixed-sex groups of up to 50 animals). Such associations are temporary. The only

Giraffe patterns display both regional characteristics as well as individual variation. Patterns shown above come from localities indicated on the map (*opposite*) and correspond to the key (*below*).

Key to Giraffe patterns:

1. Nubian Giraffe *G. (c.) camelopardalis*
2. Reticulated Giraffe *G. (c.) reticulata* (dark morph)
3. Reticulated Giraffe *G. (c.) reticulata* (light morph)
4. West African Giraffe *G. (c.) peralta*
5. Hybrid Reticulated Giraffe *G. (c.) reticulata* × Masai Giraffe *G. (c.) tippelskirchi* (between Tana and Galana Rivers)
6. Masai Giraffe *G. (c.) tippelskirchi* (light morph)
7. Nubian Giraffe *G. (c.) camelopardalis* (dark morph) '*cottoni*'
8. Nubian Giraffe *G. (c.) camelopardalis* '*rothschildi*'
9. Masai Giraffe *G. (c.) tippelskirchi* (dark morph)
10. Angola Giraffe *G. (c.) angolensis*
11. Cape Giraffe *G. (c.) giraffa*
12. Masai Giraffe *G. (c.) tippelskirchi*

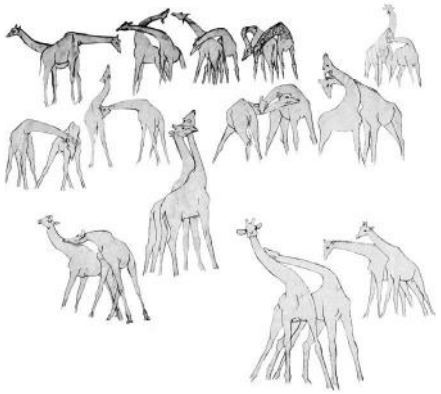
stable associations of a female Giraffe's life are the year-long periods of motherhood and the traditional, highly localised, calving area to which she returns again and again to give birth.

Gestation lasts 14 months. An oestrous female may attract close attention from many males but the majority of matings are with one or other of a few very large males. These tend to be spaced

various Giraffe postures

out within her current range. Newborn calves rise to their feet within 5 minutes and after a week or so may join up to nine other very young calves also born in the vicinity. One or more mothers are often nearby, although they tend to leave the 'crêche' of youngsters on their own during the middle of the day (the time of day when they feed most intensively and when most predators are inactive). Lactation lasts from 6 to 12 months and the young remain close to the crêche for 3–4 months, after which they begin to accompany their mothers for gradually increasing periods of time. By 6 months a calf is moving independently with adults.

Between half and three-quarters of all Giraffes fail to survive their first year. The main cause of death is predation from Lions, hyaenas, Leopards, crocodiles and humans. Their fearlessness and independence render them easy prey. Male calves are especially vulnerable because they remain in groups for 3–4 years before gradually becoming more solitary and localised. Their preoccupation



Neck sparring and fighting in male Giraffes.

with 'necking' may prejudice their survival still further.

Necking behaviour in young males tends to result in some sort of hierarchy or *modus vivendi* being established among them. These contests of strength involve rival males standing shoulder to shoulder, straining against each other, seeking to gain purchase in order to deliver and counter periodic arching blows of the head. The apparently languid pace is misleading – the necks and jaws of adult giraffes are occasionally broken in such contests and one blow has been seen to launch an adult eland into the air. By the time survivors are fully mature (at about 10 years) they are likely to have become more residential and reduced their range. Ranges narrow especially in the dry season, the peak season for conceptions.

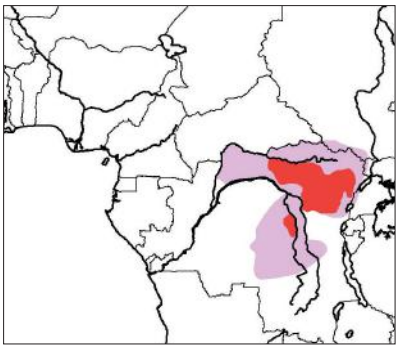
ADAPTATIONS The long neck of the Giraffe has involved a number of physiological and anatomical changes. The shoulders are deep and muscular, the thoracic vertebrae are exceptionally long in order to carry strong ligaments and the circulatory system has had to evolve very elastic vessels as well as valves to offset the sudden build-up of blood pressure whenever the head swings.

The exceptionally fast growth of Giraffes (animals double their height in 12 months) probably represents an early evolutionary strategy whereby very large, but relatively defenceless, animals were able to mitigate predation by growing too large for predators to overpower. A vast and nutritious food supply and the ability to sustain high levels of predation from carnivores was probably shared with those other giraffe species that became extinct in relatively recent eras.

STATUS Giraffes are now restricted to protected conservation areas and a few sparsely populated regions and their range continues to contract. Giraffe densities and biomass vary but, in optimal habitats, densities of up to two Giraffes per km^2 (a biomass of 2,000kg per km^2) are sustainable without prejudicing the much higher densities of other grazers on the same land. This resource could be returned to many regions if more rational patterns of land-use were devised than those imposed by currently blinkered pastoral and livestock interests. While some southern and eastern Giraffe taxa are not yet threatened, all Sahelian forms face extinction.

OKAPI *Okapia johnstoni*

OTHER NAMES Fr. *Okapi*. Ger. *Okapi*.
MEASUREMENTS HB 1.90–2.15m. T 300–560mm. W 210–356kg.
RECOGNITION A rotund, tall-shouldered ungulate with robust legs, a thick neck, large ears and an exceptionally long, mobile tongue. The hornless females are chocolate to chestnut-brown with bold black-and-white markings on the legs and white stripes radiating out from the genital area across the rump. Males are similarly marked but smaller and darker, some almost purplish black. They have swept-back, skin-covered 'horns' above the eyes. A mane, prominent in juveniles, is reduced or absent in most adults.



Okapi

DISTRIBUTION NE DR Congo and (formerly) Bwamba, Uganda. Mainly associated with minor tributaries of the NE DR Congo river basin at altitudes above 500m. It is absent from lower-lying parts of the basin and prefers firm ground. Fossils suggest that Okapis or close relatives were formerly more widespread. The spread of fire, antelopes and prehistoric hunting may have combined to extirpate them.

Okapi

HABITAT Dense, low undergrowth within the rainforest belt in river valleys, chablis and on higher ground in the wet season.

FOOD Shade-loving plants in the undergrowth; also fruits, ferns and fungi. Violet-shrubs (*Rinorea*) and *Drypetes* (a common tree) are reported favourite foods. Single leaves or entire twigs are plucked with the long, muscular, blue-black tongue. The Okapi maintains a very consistent diet and browsing routine throughout the year.

BEHAVIOUR Although of a restricted distribution and scarce over most of its range, the Okapi is common in some localities, reaching 1–2.5 per km^2. Female home-ranges average $5km^2$. Males range over a much wider area and some male territorial behaviour is suspected. They snort loudly when disturbed and make coughs and a piping sound. A female remains in oestrus for as long as a month, during which time she is closely attended by a male. Both show frequent aggression, interrupted by much rubbing, circling and head-tossing. There is an oestrus want call. Fighting males wrestle with their necks but also charge and butt one another. One precocious young is born after a 427–457-day gestation. The calf maintains contact with the mother by coughs, bleats and whistles but remains hidden; the mother goes to suckle it when called. Calves are weaned by 6 months. Male horns develop at between 1 and 5 years. Females are sexually mature at 3 years. The Okapi lives for 15–20 years.

ADAPTATIONS The disposition of pattern differs fundamentally from that found in many bovids. The Okapi has neutrally coloured ears and neck, dark fronts to the forelegs and is rather dull and inconspicuous from the front. In contrast, the tail view is truly startling. Infancy and courtship (both involving close following) are the only major departures from a mainly solitary existence. Conditioning in infancy may serve to make the optical impression created by the stripes powerfully attractive, thus offsetting aggressive or anti-social behaviour.

STATUS The Okapi has enjoyed absolute protection since 1933. The emergence of a massive commercial bushmeat trade in DR Congo now threatens it in all parts of its range. Reintroduction to Uganda's national parks should be considered if the government can be persuaded to take conservation more seriously.

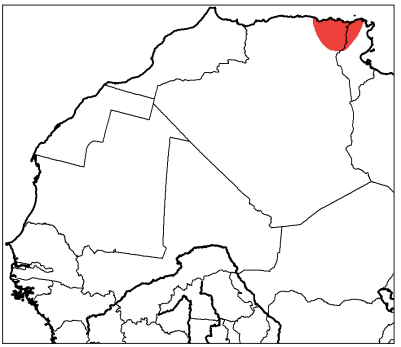
DEER Cervidae

Deer are a non-African line of ruminants that resembles antelopes very closely in body proportions and ecological niches. The most primitive species have sharp tusks like chevrotains. More advanced forms have tusks and small antlers that serve as defensive weapons against wounding by canines. In other species antlers have acquired elaborate branched structures and secondary uses in head-to-head clashes and 'wrestling'. Unlike the fixed horns of bovids, antlers are shed each year (their fast annual growth has physiological resemblances to forms of wound-healing processes, which suggests that antlers may have evolved from a type of scar-tissue). Species vary in the degree to which the side-toes have been reduced.

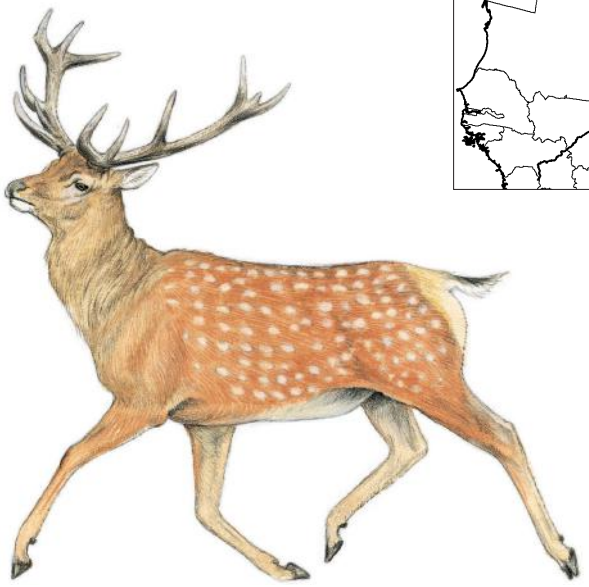
Deer digestive systems parallel those of bovids in having diverged in order to cope with difficult diets, but differ in structural details. Both cervids and bovids are the most recently evolved of ungulates. The former are widely distributed over Eurasia and the Americas but are most diverse in South-East Asia and South America. Red Deer have been in North Africa no more than 1 million years and there is no evidence to suggest that other species colonised any other part of Africa.

RED DEER *Cervus elaphus*

OTHER NAMES Fr. *Cerf élaphe*. Ger. *Hirsch*.
MEASUREMENTS HB 1.6–2.5m. T 120–150mm. Sh. ht 0.9–1.4m. W 100–150kg (♀), 150–225kg (♂).
RECOGNITION A large, long-legged antelope-like ungulate. Females are without head weapons. The larger males also lack them, briefly, in spring but grow prolonged bone-like 'antlers' over the summer months. Antler 'velvet' is shed in late summer and the antlers are used as weapons only in the short autumn 'rut' or mating season. The winter coat is dark brown with longish hair. After the spring moult the shorter summer coat is lighter reddish with pale spots. The rump is yellowish. There are scent glands in front of the eyes, under the tail, between the hooves and behind the hocks.
GEOGRAPHIC VARIATION Barbary Red Deer, *C. e. barbarus,* is the only race in Africa.
DISTRIBUTION Known as fossils from Morocco to Tunisia for nearly 1 million years. Probable relicts of that population are now only found in the Medjerda Mts on the Algeria–Tunisia border. Their greatest resemblance appears to be to Corsican deer.



Red Deer



HABITAT Cork oak and wild olive forests growing on sandy mountain soils. Red Deer remain in the woods during the day, only emerging into the open at night. The habitat is a mosaic of oak woodland, maquis and grassy meadows. Wallows are used in the summer, while moulting and during the rut (males).
FOOD Shoots of trees and shrubs, bark, young twigs, grasses, sedges and herbs; also fungi and cultivated crops. In spring and summer Red Deer enter fields and vineyards (at night or in the early morning). They are most active around dawn and dusk.
BEHAVIOUR Males and females live largely separate existences outside the rutting season. Females tend to be very residential. Male gatherings are strongly hierarchical, even for the period the animals are without antlers. The rut, which is noisy and conspicuous in many parts of their range, tends to be more cryptic in North Africa, possibly as a response to hunting. All copulations are monopolised by dominant males. After a gestation of 235 days, young are born in May and June. They tend to 'freeze' or hide when disturbed during the first 2 months. After moulting an infant coat they grow and develop rapidly, moult again into their winter coat and continue taking milk for about 7 months. They are sexually mature at 18 months (but males can seldom win mates while still young). They live for about 15 years (rarely up to 25 years).
ADAPTATIONS Long-term studies on Red Deer have shown that fewer than five surviving calves are the average lifetime offspring for each sex. However, males that win more fights get more mates and have been found to sire up to 24 offspring (about twice the maximum for females). This massive success of the winning stags is the outcome of intense male competition squeezed into the few weeks of the rut. It is antlers (backed up by brawn and drive) that allow stags to win fights but outside the rut antlers have limited use. Were antlers permanent, frequent damage would eliminate otherwise healthy contestants. Each year's regrowth progressively enlarges and adds more branches to the antlers, thereby improving the chances of their owner winning fights and siring more offspring. It is therefore likely that large antlers were elaborated in the context of strongly seasonal breeding.
STATUS Although deer have been introduced from Europe to both Morocco and South Africa, the Medjerda population is the only one thought to represent a stock that has occupied NW Africa uninterruptedly since the Pleistocene. They are protected on both sides of the border, in the El Kala NP in Algeria and the Feijja NP in Tunisia.

BOVIDS, HORNED UNGULATES BOVIDAE

Bovines	Bovinae
Antelopes, goats and sheep	Antilopinae

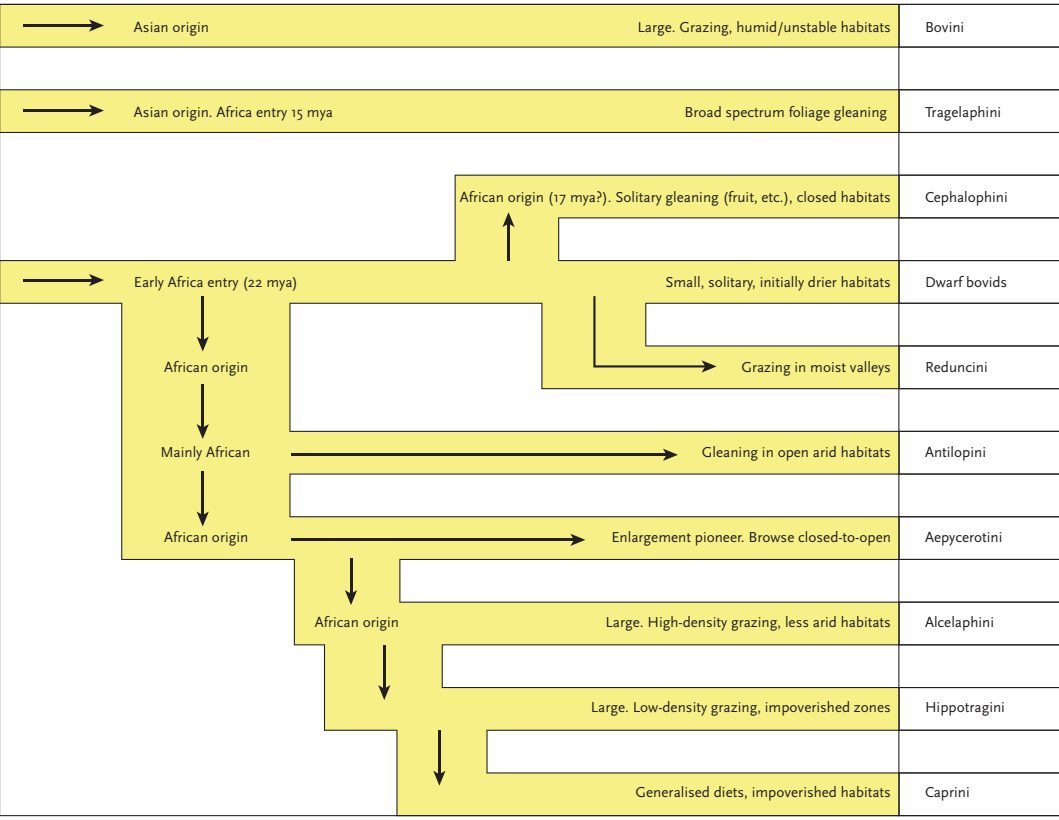
RECOGNITION Horned ungulates are long-legged, hooved herbivores that range in size from the 2kg Pygmy Antelope to the 1,000kg elands. The males of most species are horned with true keratinous horn sheaths over bony cores. In some species, females are hornless; in others, females also have horns (but never as heavy as in males). Most antelopes have a variety of scent glands. Most have horizontally oriented pupils. They come in a great variety of coat colours and patterns. All horned ungulates ruminate but food preferences vary widely: green-leaf-eating and dry-grass-eating are extremes (with fruit-eating duikers a specialised offshoot).
GENEALOGY Of Eurasian origin, both conservative Asian and African spiral-horned bovines are less well adapted to very dry habitats than the more arid-adapted true antelopes, or Antilopinae, which are now mainly African (although of ultimate Asian origin). Antilopinae have evolved a highly efficient water-saving and cooling mechanism in the nose while the more conservative bovines rely on water-wasting sweat to cool down.
GEOGRAPHY While Eurasia was home to the most primitive living bovids (called the boselaphines) and to the earliest fossils, bovids entered Africa more than once. Thus a small ancestral antelope was the earliest immigrant (more than 20 mya); an ancestral spiral-horned bovine came next (about 15–18 mya) while buffalo and caprines were still later (about 6 mya and 1.5 mya respectively) immigrants from Eurasia. The latter, sheep and goats, derived from an early African antelope but returned to Asia where, in the face of much competition from deer, they became mountain-dwelling specialists. The other antelope tribes are mostly African. The more arid-adapted groups have been better able to move between continents because corridors were usually relatively dry.

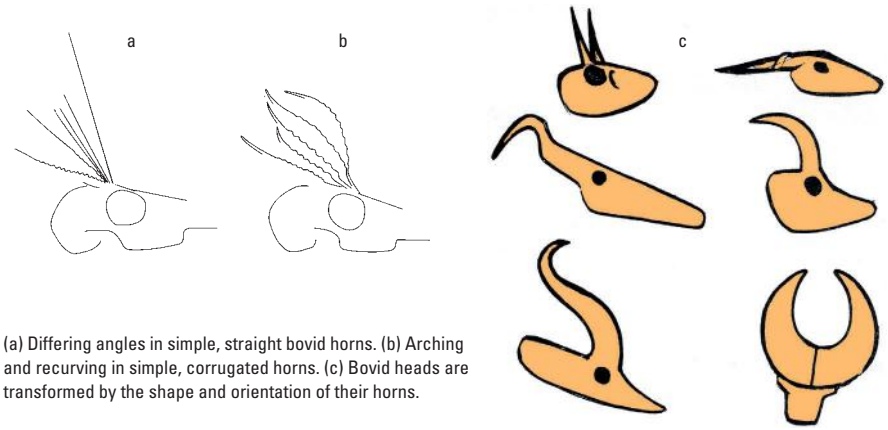
ECOLOGY Advanced rumination is the central adaptation of bovids. It could not have developed in very active animals forced to make frequent and varied demands on their metabolism. The more conservative species live solitarily in small, well-known territories where they can pick food, swallow it and then retire to chew the cud. This ecological strategy would have typified the earliest bovids. Specialisation in grass-eating came much later and developed in parallel among several bovine and antilopine lineages.

NATURAL HISTORY The need for more efficient weapons helps to explain the development of horns. A most important difference between chevrotains and bovids is the loss of tusks in the latter, leaving the mouth wholly devoted to food-gathering. In the male, simple, short, sharp 'head spikes' replaced tusks as weapons and helped protect his exclusive access to one or more females. Subsequently horns have elaborated until they have totally transformed the architecture of bovid heads. Every type of horn is wielded according to appropriate fighting and defensive techniques. Most species are annual breeders with births tending to peak in the wet season. Bovids produce well-developed young that may remain hidden for a while or, in advanced species, are sufficiently strong to run after their mothers within hours of their birth.

ADAPTATIONS The grosser differences between bovines and antelopes concern thermoregulation, gland structures and horn types. The divergence probably began with a basal bovine stock in cooler Eurasia responding to unstable seasonal habitats by enlarging its body size and becoming nomadic. In Africa improved heat and drought resistance was linked at first with small body sizes. These features permitted stable home-ranges and year-round territories.

Diversification by habitat of Bovinae and Antilopinae.





(a) Differing angles in simple, straight bovid horns. (b) Arching and recurving in simple, corrugated horns. (c) Bovid heads are transformed by the shape and orientation of their horns.

Scent signals are augmented by a variety of loud barks, whistles, moos and trumpetings. Visual signals are also important, with heads, ears, legs and rumps marked with various contrasting patches which are flagged or flashed in appropriate contexts.

The development of hard cellulose digestion (grass-eating) from the universal 'nitrogen-metabolism' type of digestion (leaf-eating), has taken place independently in at least six of the 10 main bovid tribes.

BOVINES Bovinae

Oxen	Bovini
Spiral-horned bovines	Tragelaphini

These animals are distinguished from antelopes by their generally larger size, an absence of facial or pedal glands, and smooth or keeled rather than annulated horns. Most are mobile and tend to form hierarchies in which males generally avoid direct confrontation. Hierarchy encourages sexual selection in favour of larger males. Females are smaller, hornless or less heavily horned than males in all bovines. The development or suppression of horns in females is neither primitive nor advanced, rather both horns and hornlessness involve different mechanisms for getting at resources. Horned females tend to resemble males in establishing hierarchies. They are also active in defending their young.

OXEN Bovini

African Buffalo	*Syncerus caffer*

Characterised by low, wide skulls with a short face and smooth horns that splay out sideways from the skull, oxen are large, heavy and short-legged, needing long periods for rumination. Old males tend to become slow and placid.

The living African Buffalo evolved from a smaller ancestral type that entered Africa 5–6 mya. Possibly aided by human predation, African Buffalo had effectively replaced a giant and very wide-horned type which was abundant and widespread from about 4 million to a few thousand years ago. It is now being replaced by domestic cattle.

Although some traditional pastoral societies were quite tolerant of wild animals and co-existed with antelopes, the modern take-over and conversion of land for livestock and the direct competition from cattle now threaten the existence of many wild animals right across Africa. Rapidly accelerating exploitation of exotic oxen and grasslands continues to raise major social, economic and political issues in Africa.

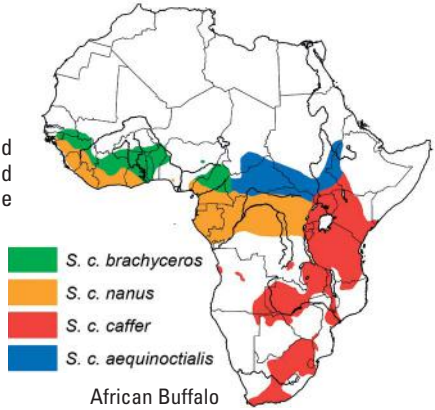
AFRICAN BUFFALO *Syncerus caffer*

OTHER NAMES Fr. *Buffle d'Afrique*. Ger. *Büffel*. Swah. *Nyati, Mbogo.*

MEASUREMENTS HB 2.25–3.40m. T 670–900mm. Sh. ht 1.0–1.7m. W 425–850kg.

RECOGNITION Large ox with thick, bossed horns and tasselled ears. The coat is short, often sparse and coloured from a rich red to black. The underside and chin is often pale (even creamy white) and patches of contrasting colour appear on the face and legs. The differences between forest and savanna forms are substantial but there are intermediate and mixed types.

GEOGRAPHIC VARIATION Western Buffalo, *S. c. brachyceros*; Forest Buffalo, *S. c. nanus*; Cape Buffalo, *S. c. caffer*; Sudanic Buffalo, *S. c. aequinoctialis*; plus the possible relict 'Mountain Buffalo', *S. c. mathewsi* (N of L. Tanganyika).



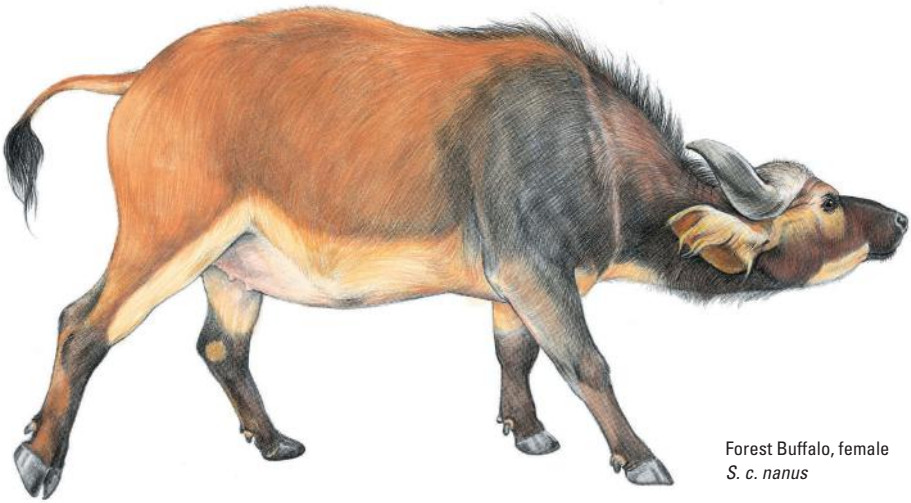
African Buffalo

Forest Buffalo are generally below 1.2m in height and 320kg in weight while the savanna forms tend to exceed these measures.

DISTRIBUTION The larger savanna forms are thought to represent recent expansion and evolution of the smaller and more conservative forest form. Until recently they ranged across all but the driest parts of sub-Saharan Africa, their local range being limited to about 20km from water. Greatly reduced by hunting and habitat loss, some populations may never have recovered from the rinderpest epidemic of the1890s.

HABITAT The Forest Buffalo depends on low-level browse and an undetermined minimum of grass in its diet, limiting it to grassy glades, watercourses and waterlogged basins. The humid climate ensures continuous plant growth which ensures that small areas will support buffalo throughout the year. Heavy browsing and grazing in 'buffalo glades' helps to limit or delay plant growth. Savanna buffalo (*brachyceros* and *caffer*) also seek out forests and valley bottoms, where possible, but can stay in the open and resist overheating and desiccation by becoming immobile or by lying in wallows. Their need for water and dense cover, as well as grass, makes them favour mosaics and savannas with patches of thicket, reeds or forest. They retain strong attachments to traditional ranges even when conditions change.

Cape Buffalo, male
S. c. caffer



Forest Buffalo, female
S. c. nanus

FOOD Grazing, breaking and trampling by buffalo favours rapid grass regrowth which encourages intense and repeated foraging. Particularly favoured grasses are *Cynodon*, *Sporobolus*, *Digitaria*, *Panicum*, *Heteropogon* and *Cenchrus* species but a wide choice of swamp vegetation is eaten. Grazing is quickly influenced by disturbance or human predation, with animals switching from continuous grazing to dawn, dusk and night-time grazing.

BEHAVIOUR The Forest Buffalo forms small groups of up to 12 animals with related females and their offspring as the core and one or more attendant males. Other males are solitary or form small bachelor parties. Savanna buffalo can assemble in much larger aggregations but similar 'family' clusters amplified into regular clan-like associations are also attended by bulls. Within these clans adults of both sexes develop hierarchical rank orders. They have well-marked seasonal breeding peaks and the dry 'off-season' sees many males breaking away from female families or clans. Gatherings of as many as 2,000 animals are only possible during the rains or on major patches of rich pasture.

Female receptivity is preceded by signs of oestrus that attract many bulls. Here the effects of male rank come into play, with the top bull or bulls having priority. Nonetheless fights are common and collisions after head-to-head charges have ended in one bull cartwheeling into the air to land on his back. Gestation lasts about 11 months and birth intervals of 2 years are normal. The cow–calf bond is very strong and exclusive but the female's attachment to her herd is also close. Thus, all adults respond to distress calls and even bulls wounded by other bulls seek refuge in the herd. Blind or three-legged animals are known to be healthy members of their family or clan. African Buffalo have been known to live for 26 years.

ADAPTATIONS The Forest Buffalo lives in habitats that do not suit large carnivores and offer easy retreat into cover. A heavy build, short legs and slow pace are therefore no disadvantage. Food is in limited, patchy but reliable supply, leading to scattered, small, resident herds. The small, back-swept horns of the Forest Buffalo reflect the infrequency of fighting and head-to-head weight-testing engagements. Increase in the frequency of fights and ever-greater selection for larger males has contributed to the rapid evolution of enormous horn bosses. When the field is free from obstruction to movement or vision, challenges are taken up from a distance and end in a full-tilt charge.

Savanna buffalo betray recent forest origins in other ways. Vision, a dominant sense in most open-country animals, is less important than sound. Quiet lowing is the preferred way of keeping in touch, especially in dark forests. This allows even blind animals to remain safe in the herd.

STATUS While this species as a whole is in no danger of extinction, its western and central African mountain forms are declining fast. Nonetheless it is well represented in numerous national parks and reserves. Not endangered.

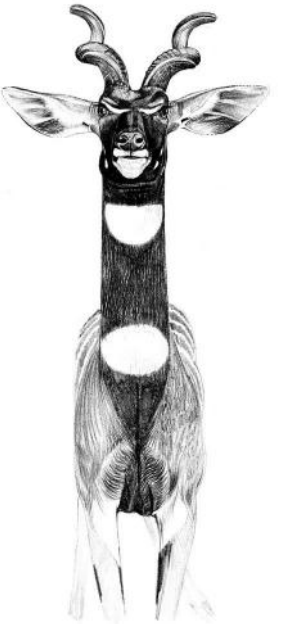
SPIRAL-HORNED BOVINES Tragelaphini

Nyalas, kudus and bushbucks	*Tragelaphus* (7 species)
Elands	*Taurotragus* (2 species)

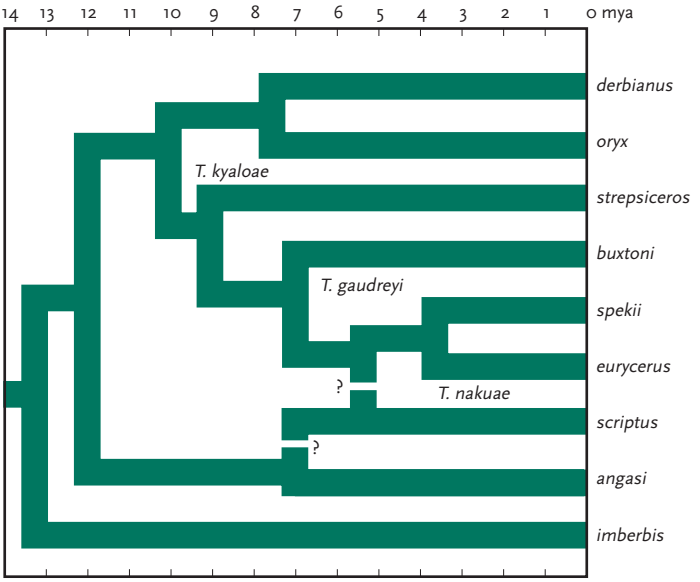
Medium-sized to large bovines with a deep body and a narrow head with big ears and twisted or spiral horns in the males. Teeth are low-crowned and, like the digestion, adapted to a diet of young, nutritious vegetation. Glandular secretions are mostly diffuse (rather than from facial or pedal pockets). The hornless females of most species have more of a generic resemblance than the larger males, which have distinctive horn shapes and darker, more contrasting coat patterns. The elands and the Bongo are 'giant' forms, with horned females.

Some zoologists used to make no distinction between tragelaphines, oxen and an Asiatic animal that resembles both, the Indian Nilghai (*Boselaphus*). Fossils suggest a common Asian origin for all three bovine groups but their African branch has been distinct for at least 15–18 million years.

In the past tragelaphines were often subdivided into various genera or sub-genera. With the advent of molecular phylogeny the consensus has been to group all tragelaphines in *Tragelaphus*. All species derive from a single immigrant ancestral type of which the earliest derivatives are the Lesser Kudu and Nyala (*T. imberbis* and *T. angasi*), both confined to dense thicket habitats. At about 10 mya a split developed between a gracile but still conservative, thicket-loving lineage and a lineage of larger size, adapted to more open habitats. Greater Kudu and the elands are descendants of this adaptive phase. The Mountain Nyala, *T. buxtoni*, is the relict of a large type sharing origins with the Greater Kudu. Still later, a forest lineage emerged giving rise to three surviving species: Bongos



Lesser Kudu, frontal view



Tentative phylogenetic tree of tragelaphine radiation (in part after Willows-Munro *et al.* 2005 and Hassanin *et al.* 2012). Note that SE and centre-west *Tragelaphus scriptus* might have separate or genetically mixed origins.

(large forest-edge descendants), Sitatungas (swamp refugees) and Bushbucks ('dwarf' morphs). Bushbucks have very complex genetics and, possibly, might represent an amalgam between an early Nyala-like descendant and a dwarfed Bongo-like lineage.

Fossil relatives (or parallel cousins) of this now exclusively African group are known from south Asia. There is still a strong eastern and southern African bias in their distribution (typical of other organisms with 'immigrant' origins).

All species are gleaners of green foliage in a wide variety of mostly unstable habitats. None tolerates true desert. Herding in the larger tragelaphines is not induced by the habitat (as it appears to be among the kobs, Reduncini) but is the defensive strategy of females and young.

Their social structures tend to be rudimentary. Vulnerability of the young is a major incentive for forming herds among the largest, most mobile species. Females are the more ready to associate, and the need to defend the young (as well as enforce rank) has influenced the development of horns in female Bongos and elands.

Males also show rank orders and sometimes live at very high densities. Rank is assessed through size-enlarging displays and may be partly cyclical. Periodic testosterone 'surges' are signalled by aggression, or *ukali*. This deters confrontations. Rare instances of all-out fighting and death may result from confrontations between well-matched males who are both in their *ukali* phase. Males of all species horn the soil, or vegetation. These are not territorial beacons but more general advertisement of status and presence.

In marked contrast to buffalo and other bovines, tragelaphines are alert and highly visual animals and visual signals are both subtle and highly structured. All species begin as striped and blotched infants that 'freeze' or hide to escape detection. They have conspicuous white flashes on ears, muzzle and lips. These function most obviously when mothers approach hidden young, at which time they bob or flag their heads up and down, sometimes calling very softly at the same time. Adult males develop ritualised broadside displays to impose upon other animals. Manes, crests, black-and-white markings and rangy, flat-sided figures all serve to enhance male displays during courtship but more especially in rank contests.

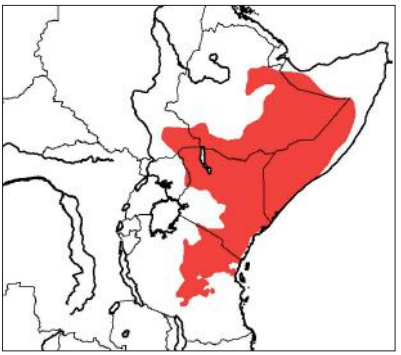
Another clue to rank is the loudness and timbre of the male barks. Visual and vocal signals appear in different permutations in four closely related species. The flamboyant Nyalas, living in mosaics of thickets laced with open corridors, valleys and glades, silently strut their frills and crests. Lesser Kudu, risking ambush in denser, drier bush, have subtle, close-contact patterns on legs, face and throat and bark sparingly. The Sitatunga, submerged in thick grass, mud or water, has vestigial or muted patterns but barks frequently, loudly and persistently. The Bushbuck is the most versatile: colourful, contrasty and Bongo-like in the forested west, it is more discretely Nyala-like in the drier, more open (and dangerous) south and east. Both sexes can be voluble.

Spiral horns have variable functions but are particularly well suited to defensive horn-wrestling. The differential growth mechanisms determining spirals are so simple that much variation is possible. Individual variations are common in some species but nonetheless the trajectory of spirals is highly species-specific.

Studies of tragelaphine brains have revealed that the Nyala (*T. angasi*) and Lesser Kudu (*T. imberbis*) have much the smallest (and presumably most primitive) brains, confirming their conservative status.

Sitatunga male head, frontal view

LESSER KUDU *Tragelaphus imberbis*



Lesser Kudu

OTHER NAMES Fr. *Petit koudou*. Ger. *Kleinkudu*. Swah. *Tandala ndogo*.

MEASUREMENTS HB 1.10–1.75m. T 250–400mm. Sh. ht 0.9–1.1m. W 56–70kg (♀), 92–108kg (♂).

RECOGNITION Females and young are bright russet, with 11–15 vertical white stripes. They have a long, narrow head and resemble the Nyala very closely, except for slightly longer legs and neck. Yearling males acquire sandy-grey colouring that is almost identical to that of similarly aged Nyala males. The black-and-white markings on face, tail and tawny-orange legs are also extremely similar in both species, with the greatest contrast in males. Although the males of both species darken with age, Lesser Kudu remain well-camouflaged by their colouring. The short and sparsely haired neck has geometric white markings on throat and chest. There are inguinal glands in the groin and secretions around the false hooves.

GEOGRAPHIC VARIATION Two subspecies described, *T. i. imberbis* (Horn of Africa), *T. i. australis* (E Africa), but apparently a continuum. A distinct form might have occurred in Arabia.

DISTRIBUTION Horn of Africa, E Ethiopia (up to 1,300m) and the drier, lower regions of Kenya and Tanzania. Formerly in S Arabia.

HABITAT Deciduous bushlands and thickets dominated by *Acacia* and *Commiphora*. Resident Lesser Kudus display some seasonal movement from the more deciduous upper slopes in the wet season to low-lying evergreen belts in the dry season.

FOOD Browsers of foliage and herbage with a strong reliance on a few evergreen species during the dry season, notably the succulents (*Calyptrotheca* and *Euphorbia*) and the Toothbrush Tree (*Salvadora persica*). Nonetheless, more than 100 species of plants have been recorded from a single locality, including sprouts (especially *Combretum* and *Cordia*), buds, leaves and pods of various *Acacia* species, flowers and fruits. Grasses are

Lesser Kudu tail flash

Lesser Kudu, male

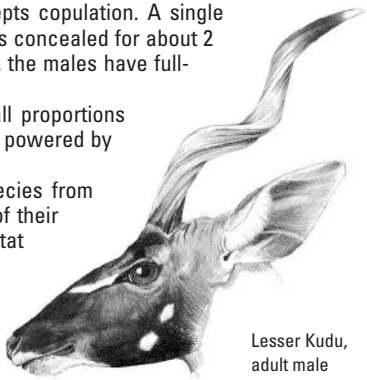
taken sparingly while green and fresh. Lesser Kudus are able to extract sufficient moisture from their food but visit water-holes or rivers where they can.

BEHAVIOUR Highly residential but non-territorial animals. Females tend to aggregate most (up to 24 in a group) and occasionally two or three females (presumably close relatives) sustain long-term companionships. Hierarchies have not been observed and all classes meet and part casually. Older males actively avoid each other except in the presence of oestrous females. Females are the most residential, with home-ranges of about 60–500ha. Newly independent males move over a larger area (up to 670ha) but gradually settle into a smaller home-range.

The normal gait is a level walk but animals can leap 2m when fleeing, throwing tail and hindquarters in the air and sometimes uttering a harsh bark as they go. Both sexes bark but this mainly serves avoidance and orientation rather than signalling alarm. There is no observable breeding peak. The male courts the female with a hicking, gasping call and whines, continually following her while rubbing and nibbling until she accepts copulation. A single young is born after about 222 days' gestation and remains concealed for about 2 weeks. Sexually mature between 18 months and 2 years, the males have full-length horns by 4 years. Lesser Kudus live for 15 years.

ADAPTATIONS Males strut and spar but their slender, tall proportions favour a form of see-sawing horn wrestling that is mainly powered by the neck and designed to bring opponents to their knees.

STATUS Extreme alertness and shyness protect this species from predators (and conceal them from would-be assessors of their status). Animals are wholly dependent on their habitat remaining relatively closed and may even benefit from overgrazing that suppresses fire. As a widespread but patchily distributed species it is not yet endangered. Nonetheless it has disappeared from a large part of its former range in Somalia.



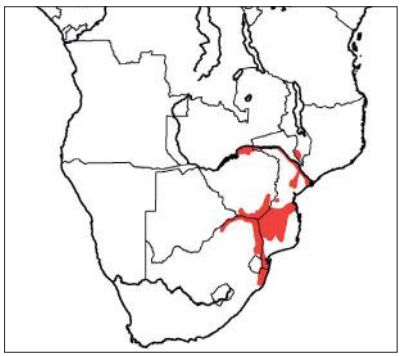
Lesser Kudu, adult male

NYALA *Tragelaphus angasi*

OTHER NAMES Fr. *Nyala*. Ger. *Tieflandnyala*.

MEASUREMENTS HB 1.32–1.46m (♀), 1.60–1.98m (♂). T 360–550mm. Sh. ht 0.8–1.05m (♀), 1.0–1.21m (♂). W 55–68kg (♀),92–126 (140?)kg (♂).

RECOGNITION Females are slender and russet with up to 18 bold white stripes down their sides. Males begin with similar colouring but pass through a prolonged metamorphosis as they mature. First they turn sandy grey and grow tufts on the chin, throat and belly. As the horns lengthen, the dorsal crest and continuous fringes of hair also grow in length. The colour darkens and the pale vertical stripes fade and may disappear altogether. The timing of all these developments varies individually and in some cases crests and colours remain relatively or absolutely undeveloped. The 'false' or side hooves are fringed with glands but Nyala lack inguinal glands in the groin. Male horns range from 400 to 835mm in length. Chunky hooves leave a distinctive spoor, with a compact, rounded margin.



Nyala

DISTRIBUTION The Nyala occupies a highly anomalous region in SE Africa where Kalahari-type sands outcrop near the east coast. The low-lying Limpopo basin, with appreciably lower rainfall than its surroundings, forms the heart of its distribution but even outside this core area well-drained soils support a similar 'lowveld' vegetation unique to the region. It does not occur above 1,400m.

HABITAT A mosaic of dense Mopane (*Colophospermum mopane*) thickets and more open woodlands, pans and scrub. Grass in the open areas tends to be ephemeral growth during the summer rains. Patchy fires help to maintain this very unstable mosaic. The Nyala uses the thickets for browsing and shelter but emerges into more open areas at night, especially during the wet season. The denser areas of its habitat resemble those in NE Africa, with bush-willows (*Combretum*), Shepherd's Tree

Nyala, subadult male

Nyala, female

Nyala, adult male

(*Boscia albitrunca*), torchwood (*Balanites*), myrobalan (*Terminalia*) and baobabs (*Adansonia*), as well as acacias.

FOOD Favoured browse species are *Acacia*, Toothbrush Trees (*Salvadora persica*), buffalo thorn (*Ziziphus*) and monkey apple (*Strychnos*). The Nyala picks up fallen leaves, herbs, cucurbits and various small legumes. During the rains fresh green grass attracts it into open areas.

BEHAVIOUR Up to 50 animals can gather on a flush of fresh growth while oestrous females can attract much smaller aggregations. Essentially independent, animals will readily meet and part with a frequency that depends on local Nyala densities. Home-ranges vary from 33 to 360ha, with an average of about 75ha. There are two slight breeding peaks but births can occur in any month. Gestation exceeds 7 months (about 220 days) and the young remain concealed for nearly 3 weeks before emerging to follow their mother and join other females for variable periods. They are sexually mature by 18 months but males are unlikely to breed until they have long horns, dark colouring and fully developed crests and tassels (at about 3 years). They live for at least 16 years.

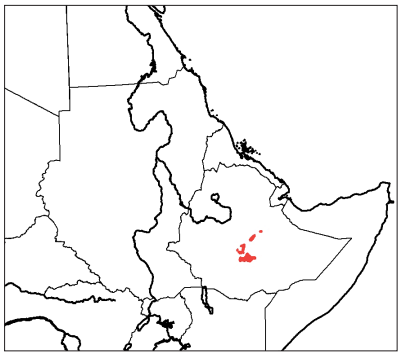
ADAPTATIONS Among bovids, Nyala males are the most extreme specialists in advertisement through visual display. Their fringes enlarge the body boundaries and dark colour increases the impression of weight and solidity. Strutting displays generally result in the subordinate male lowering his head and crest as he quietly withdraws. Rare fights with the horns are all-out and can cause death or serious wounding.

STATUS Currently satisfactory, as it is represented in good numbers in many parks and reserves. The Nyala is also a common zoo animal. Its habitat has rather low agricultural value although this could change with the provision of irrigation. Not endangered.

MOUNTAIN NYALA *Tragelaphus buxtoni*

OTHER NAMES Gedemsa. Fr. *Nyala de montagne*. Ger. *Bergnyala*.

MEASUREMENTS HB 1.9–2.0m (♀), 2.4–2.6m (♂). T 200–250mm. Sh. ht 0.9–1.0m (♀), 1.20–1.35m (♂). W 150–200kg (♀),180–300kg (♂).

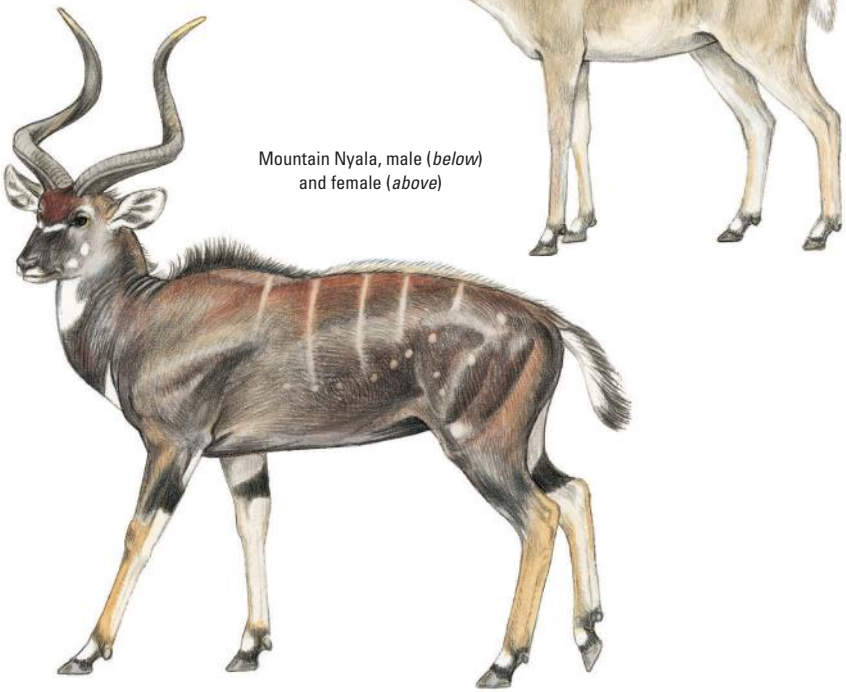


Mountain Nyala

RECOGNITION In general proportions and size, the hornless female Mountain Nyala resembles a Red Deer hind. The females are of a pale liver colour, with paler undersides and a scatter of vestigial spots and stripes. The horned adult males can be nearly twice as heavy, with deep chests, a dorsal crest and body colour of sepia brown that slowly gets darker with age. This throws white markings on the ears, face, throat, chest and forelegs into strong relief. The males can be smooth and glossy or can become quite shaggy during the cold season. The tightness of the horns' spiral, and their thickness and length, vary; they can measure up to 1.18m along the curve.

DISTRIBUTION Formerly ranging all over the SE highlands of Ethiopia from Ch'erch'er Mts to Sidamo before being exterminated; now limited to the Bale massif. Ranges from 3,000 up to 4,200m but stragglers occur as low as 1,800m.

HABITAT Until very recently it flourished best in a mosaic of high-altitude woodland, bush, heath, moorland and valley-bottom grassland. The woodlands (mostly juniper and *Hagenia*), heath and bush (dominated by sage brush,

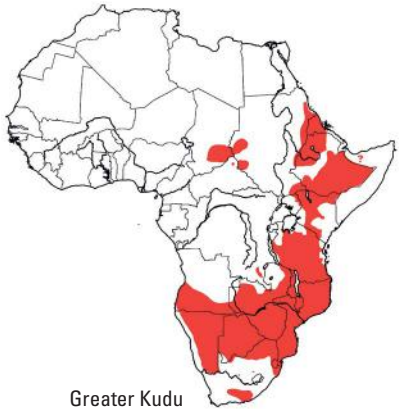


Mountain Nyala, male (*below*) and female (*above*)

Artemesia and everlasting, *Helichrysum*) provide dry-season refuge. With the rains there is a greater choice of pasture at lower levels (a similar pattern found with the Bongo in mountains). The sedgy grasslands tend to be waterlogged and animals have even been seen eating water-plants.
FOOD Herbs and shrubs with occasional grass, lichens and ferns. The most frequent browse is plants of the tomato family (Solanaceae), St John's wort (*Hypericum*), lady's mantle (*Alchemilla*) and goosegrass (*Galium*). The Mountain Nyala eats fallen leaves of *Hagenia* during the dry season.
BEHAVIOUR Females accompanied by one or two generations of young form very frequent but essentially impermanent associations with other mother–young groups. These are regularly joined or monitored by adult males. Numbering up to 13, such groupings tend to be smaller in the dry season when they range very widely. Females restrict their movements in the rains to about 5km^2. Males, instead, range as widely as 20km^2. Young males are more mobile and less solitary than the older males and determine local hierarchies with frequent horn-wrestling contests. Older males are more prone to slow, circling displays with raised crests. Once one male begins to drop his head the engagement is broken off and the subordinate departs. There is a mating peak in about December and single young are born after an 8–9-month gestation, at the end of the wet season. The ochre-coloured young lie up for a couple of weeks and then stay closely attached to their mother for as long as 2 years, by which time female calves are themselves pregnant and males have long horns and join bachelor groups.
ADAPTATIONS The lowlands surrounding the Bale massif are inhabited by Greater Kudu and it is very likely that this more arid-adapted and more agile species outcompetes the Mountain Nyala in these habitats. Adaptation to extreme temperature oscillations and a more limited diet of specialised montane vegetation is probably the product of their prior occupation (by some millions of years) in the region. While their ancestors had a wider span of habitats (before the evolution of Greater Kudu) they have now become montane specialists in their diet and physiology.
STATUS On present showing, this pivotal species in tragelaphine evolution faces extinction. A total population estimated at 12,500 in the 1960s was reduced by 1988 to 2,000–4,000 animals, but at least half this population was restricted to a small part of Bale NP (where they reached densities of more than 20 animals per km^2). From 1991, two decades of official folly have combined with gross environmental mismanagement to shatter Ethiopia's conservation estate. While licences to kill Mountain Nyalas and other 'game' animals are still easily available, study of and education about the country's natural resources and their maintenance are neglected. Export of live animals is forbidden, yet sustained captive breeding by responsible agencies has become the last best hope for this and other Ethiopian species. In the face of appalling official inertia, past proposals for the establishment of protected satellite populations in the Arssi and Harerghe Mts and elsewhere have become inconsequential. IUCN rates the species as endangered.

GREATER KUDU *Tragelaphus strepsiceros*

OTHER NAMES Fr. *Grand koudou.* Ger. *Grosskudu.* Swah. *Tandala.*
MEASUREMENTS HB 1.85–2.35m (♀), 1.95–2.45cm (♂). T 300–550m. Sh. ht 1.0–1.4m (♀),1.22–1.50m (♂). W 120–215kg (♀); 190–315kg (♂).
RECOGNITION A tall dun-coloured bovine with 4–12 pale stripes on the body and spiral horns reaching a record length of 1.81m (along the curve) in males. Both sexes have a crest down the middle of the back and a mane. Males have a tesselated dewlap. Females vary in colour from sandy yellowish-grey to russet, males tend to be greyer. Females are normally hornless. Both sexes have very large, rounded ears. All living forms are substantially smaller than Pleistocene Greater Kudus.


Greater Kudu

GEOGRAPHIC VARIATION *T. s. strepsiceros* (S and E Africa), *T. s. chora* (NE Africa), *T. s. cottoni* (Chad to W Sudan).
DISTRIBUTION Originally from the mountains of SE Chad to Ethiopia and throughout the drier areas of East and southern Africa, wherever there were thickets and dense woodlands to provide

Greater Kudu, male in strutting posture

browse and shelter. Greater Kudus are increasingly restricted to stony, hilly country by expanding settlement. They can survive without water if browse is sufficiently moist.

HABITAT Thickets and evergreen forests along watercourses and on cloudy heights provide dry-season refuges. In the wet season they disperse through deciduous woodlands and may emerge at night to graze off herbs and grass on open *Acacia*/*Commiphora* pans. Their long legs and necks allow them to browse to greater heights, exceeded only by the giraffe.

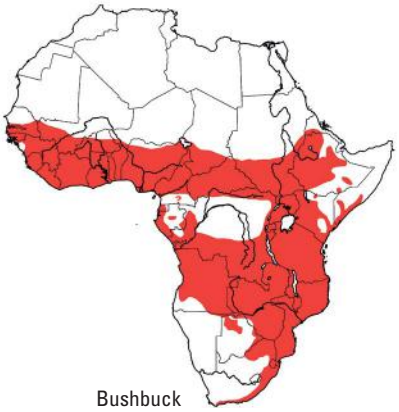
FOOD A very wide range of foliage, herbs, vines, flowers, fruits, succulents and grass. There are striking seasonal changes in diet, with trailing morning glory (*Ipomoea*), vines (*Vigna*), firebush (*Hymenodictyon*), lucky bean (*Abrus*) and bean trees (*Markhamia*) being typical wet-season browse. Choice is much more restricted in the dry season but Sodom Apple (*Calotropis procera*), buffalo thorn (*Ziziphus*), *Acacia*, *Aloe*, *Cassia* and *Cadaba* are staples, while the slow leaf-fall of bush-willows (*Combretum*) provides browse well into the dry season.

BEHAVIOUR Wide dispersion during the rains tends to separate the sexes and there is a mating peak during the dry season when animals return to the core of their range in valley thickets. Groups of 2–25 typically include several adult females with offspring of both sexes. Although parties mingle and separate frequently, some individuals form loose associations that last from one year to the next. Males also return to the same refuges every dry season. Here several clusters of females regularly share the home-range of a dominant bull (which averages about 10km^2). Such males are not territorial but they drive off any males attempting to consort with their current female companions.

Adults utter very loud and startling barks; males grunt when fighting or during confrontations. A hooting bleat signifies distress and a courting male makes a strangulated whimper as he persistently follows and nudges the female. Gestation lasts 9 months; the young lies up for about 3 weeks and is weaned and fairly independent by 6 months but remains in touch for up to 2 years. Females are sexually mature by 3 years, males by 5 years (their horns reach full length by 6 years). Greater Kudus have lived for 23 years in captivity.

ADAPTATIONS There is a relationship between the Greater Kudu's height and the great length of its horns because they have to shield the body of a sparring male. Contestants engage their spirals in order to make a firm link-up before pushing and trying to throw one another off balance. The spiral structure relates to this wrestling technique but the horns are also visual symbols of rank that may influence female preferences or choice for mating.
STATUS The Greater Kudu is rare in some peripheral parts of its range. It is endangered in Somalia and Uganda and is thought to be vulnerable in Chad and Kenya. Its overall range in Tanzania continues to contract, but Greater Kudus are still widespread and well represented in national parks and reserves, especially in southern Africa. Not endangered.

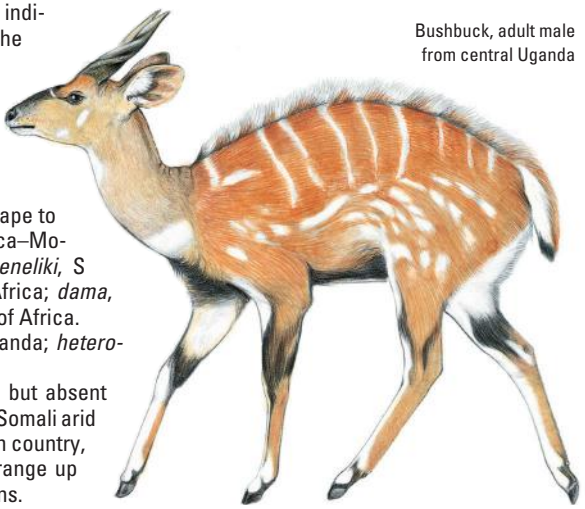
BUSHBUCK *Tragelaphus scriptus*


Bushbuck

OTHER NAMES Fr. *Guib harnaché*, *Guib*. Ger. *Schirrantilope*. Swah. *Mbawala*, *Pongo*.
MEASUREMENTS HB 1.14–1.50m. T 190–250mm. Sh. ht 0.61–1.00m. W 24–60kg (♀); 30–54 (80?)kg (♂).
RECOGNITION A small bovine, the Bushbuck converges with many antelope and deer in having average proportions. Females and young are mainly red and males become progressively darker with sexual maturity and age. Both sexes and all ages have a white underside to the broad, woolly tail, white flashes above black hooves and white markings on face and ears. Western forest forms are 'harnessed', with both vertical and horizontal white body stripes and numerous spots on the haunches. Eastern and southern 'sylvan' populations are sometimes plain and often sparsely marked with a few light spots or streaks on flanks or haunches. In central Africa there is a broad polymorphic belt. Genetic studies have opened the possibility of one ancestral source (*scriptus*) in the west, another (*sylvaticus*) in the south, in which case at least two species (and perhaps a hybrid swarm, too) would be called for. Much more research is needed before any informed taxonomy can emerge.

The male's horns are 250–570mm long and vary from being very short, thick and nearly straight to longer and thinner with two marked kinks in the spiral. Montane and forest forms are blacker and/or redder while those from the driest areas are yellower. In between are intermediate tints. Pale dorsal crests are present in most populations. Necks and faces are short-haired in most areas but hairy in some montane populations.

GEOGRAPHIC VARIATION Much individual variation has influenced the naming of some 27 subspecies; a selection is listed below:
Harnessed antelopes: *scriptus*, Upper Guinea; *phaleratus*, Bight of Benin; *bor*, east-central Africa; *decula*, N Ethiopia.
Bushbuck antelopes: *sylvaticus*, Cape to KwaZulu-Natal; *roualeyni*, SE Africa–Mozambique; *delameri*, E Africa; *meneliki*, S Ethiopia; *ornatus*, south-central Africa; *dama*, L. Victoria region; *fasciatus*, Horn of Africa.
Montane isolates: *barkeri*, NE Uganda; *heterochrous*, Mt Elgon.


Bushbuck, adult male from central Uganda

DISTRIBUTION Sub-Saharan Africa but absent from the south-west, Kalahari and Somali arid regions. Locally absent in dry, open country, they are water-dependent. They range up to 3,000m on East African mountains.

Bushbuck polymorphism.

Key:

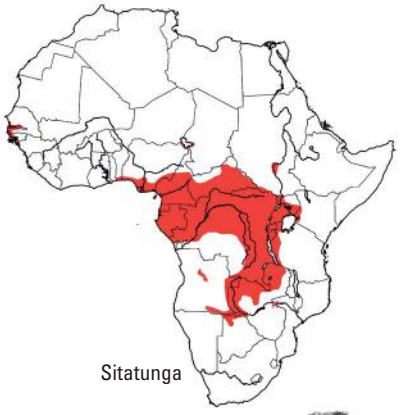
1 A dark morph of West African *scriptus* male
2 West African *scriptus* male
3 West African *scriptus* female
4 A light morph of West African *scriptus* male
5, 6, 7 Three males from a single locality (Kasulu, Tanzania) to show variation in pattern and colour (*dama*)
8 Pale male from Ujiji, Tanzania (*dama*)
9 Ethiopian Mts male (*menelikí*)
10 Pale male from Moyale, North Kenya
11, (11.2), 12, 13 Four animals from a single high-altitude locality (Mt Elgon) (11 and 11.2: female and her young) (*heterochrous*)
14 Male from Fort Portal, Uganda (*dama*)

HABITAT Essentially dependent on thick cover, even if this is no more than small thickets centring on termitaries. They need water but can subsist on dew. They sometimes live in reedbeds.
FOOD Largely shrubs, leguminous herbs and growing grass (often a nocturnal preference); also pods, fruits of many species. Feeding patterns are strongly influenced by disturbance and predators. Frequently resting and ruminating, Bushbucks are strictly solitary, even if they feed close to other Bushbucks.
BEHAVIOUR Living at very variable densities, the males appear to maintain linear hierarchies where both colour-coded age grades and *ukali* (testosterone surges) may influence individual status. Although normally very residential they are not territorial, even at densities of up to 26 per km^2 (on a fertile bushy peninsula). Deaths, the incursion of immigrants, maturation of males and coming into season of females are potentially disruptive. Females form regular associations with other females and a smaller number of males that live in the same area (and are likely to be close relatives).

One young is born after a gestation of about 6 months. Infants keep well hidden for up to 4 months and mature by 1 year, although male horns reach adult size only at about 3 years (at which time colouring and behaviour also change). They live for 12 years or more.
ADAPTATIONS The survival of Bushbucks in settled, agricultural areas and their very wide distribution imply that their smaller size and 'freezing' and crouching strategy help conceal them from both humans and carnivores. A versatile diet and ability to subsist on both grass and browse also contribute to their success. Males have a very loud, deep, roaring bark that serves to mob or even intimidate predators, as well as to challenge or alert other Bushbucks. Females also bark but less loudly and less frequently. When uttered repeatedly by a moving animal, barks indicate change and movement. Neighbouring Bushbucks scarcely ever bark in response but usually change direction or seek shelter. Males utter a twittering call while courting.
STATUS Isolated mountain morphs, such as the Mt Elgon and N Uganda forms (*T. s. heterochrous* and *T. s. barkeri*), are locally vulnerable but overall Bushbucks remain common and widespread.

SITATUNGA *Tragelaphus spekii*

OTHER NAMES Fr. *Sitatunga*. Ger. *Sumpfantilope*. Swah. *Nzohe*.
MEASUREMENTS HB 1.04–1.46m (♀), 1.36–1.77m (♂). T 140–370mm. Sh. ht 0.75–1.05m (♀), 0.85–1.25m (♂). W 24–57kg (♀), 76–119 (130?)kg (♂).
RECOGNITION A shaggy, long-legged bovine distinguished by its long, splayed hooves and somewhat spread-eagled stance (both adaptations to living on boggy ground). The hornless females resemble other tragelaphines and are rufous with eight or ten white dorsal stripes. Males are larger and darker, with heavy, sharply keeled horns measuring 450–920mm. They describe a shallow spiral with one and a half twists. Deep, muscled cheeks contrast with a relatively short and slender muzzle.
GEOGRAPHIC VARIATION Nile Sitatunga – *T. spekii spekii* (Nile watershed); Congo Sitatunga – *T. s. gratus* (W and central Africa); Southern Sitatunga – *T. s. selousi* (southern Africa).
DISTRIBUTION The primary habitat and centre of Sitatunga distribution is the Congo basin (where the ancestral population probably adapted to the shores and tributaries of the former Congo Lake). Populations in the Niger and other river basins west of this region have been allocated to the same subspecies (*T. s. gratus*). Distinct populations inhabit swamps, lakeshores and valley bottoms centred on the R. Nile and R. Zambezi/R. Bangweulu drainage basins.
HABITAT Adaptation to a grassy diet and open swamps is secondary to inhabiting the more complex communities of shrubby growth, herbs, sedges, grasses and palms that border forest waterways.


Sitatunga

female

Eastern, southern and far western parts of their range are dominated by extensive beds of reeds (*Echinochloa*), bullrushes (*Typha*) and sedge or papyrus (*Cyperus*).

FOOD Shrubs, herbs and grasses with strong regional biases; *Monodora*, *Uvaria*, *Xylopia* and *Alchornia* species are favourite browse in Uganda, swamp grasses and sedges in Bangweulu, Okavango and the Sudd. Some flowering plants are especially favoured. Sitatungas often feed very intensively in a small area for some days or even weeks and then desert it. They are most active from 18.00 to 10.00, but are less restricted in undisturbed swamps.

BEHAVIOUR A rich, year-round supply of greenery permits exceptionally small home-ranges and potentially high densities. On Nkosi, a small, wooded island in L. Victoria, densities once reached about 200 per km^2 and 55 per km^2 have been reported elsewhere. Temporary aggregations gather for a few hours on favourite pastures only to disperse. Females are especially prone to gather in high-density areas and may be accompanied by more than one generation of calves. They have a clumsy gait but are quiet and deliberate in their movements. They avoid attention by cautiously entering thick vegetation and sink down into water very slowly, leaving only the snout and part of the head above the surface.

Crescendos of barking are common at night in high-density areas, especially after a disturbance, and sometimes stimulate more than one barker. If listening males can discern age and vigour from the timbre of a bark, such calling could reduce the likelihood of lethal fights. Courtship resembles that of other tragelaphines. Gestation lasts more than 7 months, with birth peaks noted in the dry season (July in E and SE Africa). One young is born on a trampled resting platform or in a 'form' in thick vegetation. It is then left on its own, except for quick visits by the mother. The female keeps hiding and suckling places separate by leading the young into dense vegetation to nurse. The young are independent and playful from an early age.

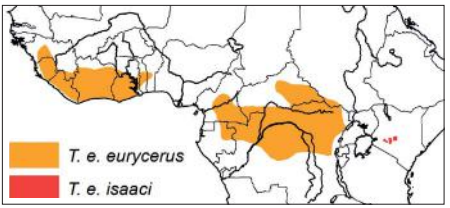
Resting and ruminating are invariably solitary. Sitatunga mature by about 4 years and captive specimens have lived for up to 20 years.

ADAPTATIONS The most striking adaptation is elongation of the hooves, which renders animals particularly clumsy on dry or broken terrain. Sitatungas emerge from swamps to wander more widely in the wet season. In the Sudd this represents a modest but discernible shift from deep permanent swamp onto the margins of a seasonal floodplain with different food plants.

STATUS Hunting may threaten Sitatungas in some marginal areas of their range. They are particularly vulnerable to persistent snaring, because they use paths and tunnels, and to wholesale burning or drainage of their habitat. However, they can withstand heavy and persistent hunting if the swamps remain intact. They are rare or endangered locally, i.e. in Kenya, L. Chad, Zimbabwe, but substantial populations of all three subspecies remain. Possibly the best suited of all tragelaphines to intensive domestication or semi-domestication. Not endangered.

Sitatunga, male (*above*) and female (*right*)

BONGO *Tragelaphus eurycerus*



Bongo

OTHER NAMES Fr. *Bongo*. Ger. *Bongo*. Swah. *Bongo, Ndongoro*.

MEASUREMENTS HB 1.7–2.5m. T 450–650mm. Sh. ht 1.1–1.3m. W 182–276kg (♀), 240–405kg (♂).

RECOGNITION Long-bodied, muscular bovine, coloured deep russet red, with 10–16 vivid white stripes on each side. Both sexes are spiral-horned with deep, flat flanks. Males have a vestigial dorsal crest and bold, black-and-white markings on the extremities. Males continue to put on weight with age and slowly darken until they are nearly black. Body proportions vary, with W African Lowland Bongo consistently smaller and shorter-legged. The Kenya Mountain Bongo is taller and much heavier. Glandular secretions appear to be dispersed over the body and are not restricted to discrete sacs or tracts.

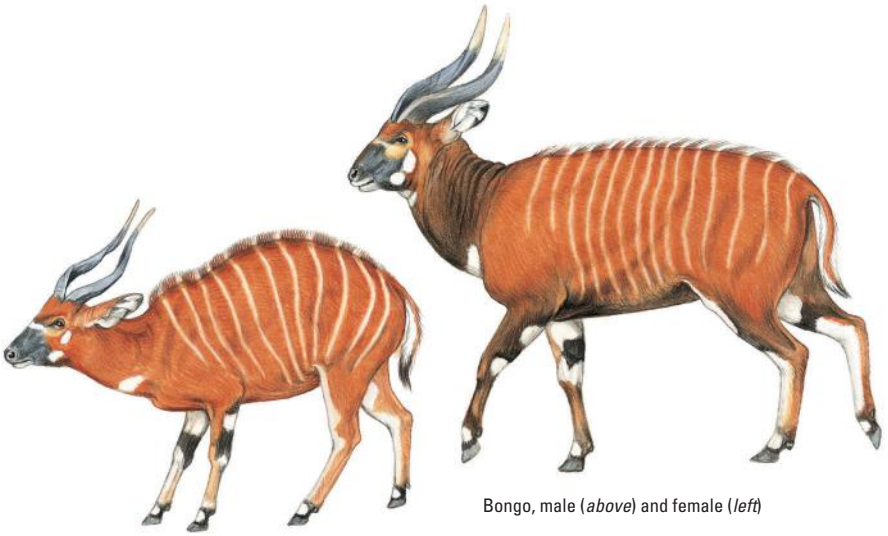
GEOGRAPHIC VARIATION Lowland Bongo, *T. e. eurycerus* (W and central African lowlands); Mountain Bongo, *T. e. isaaci* (Kenya highlands only).

DISTRIBUTION Restricted to forest mosaics on or north of the Equator. Bongos occur patchily from Sierra Leone to Mt Kenya. Like all tragelaphines, they are adapted to unstable habitats. In Kenya they prefer slopes between 2,000 and 3,000m, ranging (in larger groups) above 2,500m up to 4,000m in the dry season and dispersing at mainly lower altitudes in the rains.

HABITAT Landslides, floods, fires, treefalls, heavy elephant-browsing, logging and fallow all favour regrowth of the low-level fresh greenery that Bongos need and they only occur in such disturbed forest mosaics. In montane areas mass die-offs of bamboo suit them. They remain relatively inactive in dense cover during the day and tend to move at night, but are always close to refuges in undergrowth or thickets.

FOOD More than 80 food plants have been recorded from a single locality. These include the foliage of shrubs and young trees, herbs, young grass and especially vines that are dragged down off trees or pulled up from the ground. Occasionally particular species become favourites: young *Albizia* seedlings, the herbs *Acalypha* and *Rinorea*, balsam (*Impatiens*) and wild yam vines (*Dioscorea*) have been noted.

BEHAVIOUR Individuals (of both sexes) do not form permanent links with others beyond the mother–young bond. Nonetheless, mothers suckling young after the latter's concealment phase seek one another out. Three months after the July–September birth peak in Kenya all lactating females are in large nursery herds where their behaviour is more confident and relaxed than when single (and


Bongo, male (*above*) and female (*left*)

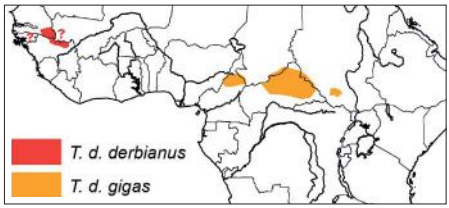
typically alert and timid). They range widely (possibly 120–300km^2) and all classes have overlapping home-ranges.

Males do not herd females nor coerce them, nor do they influence their movements or groupings. Typically scattered dispersal favours efficient tracking and testing of females rather than direct competition for isolated, unpredictable mating opportunities. Body odours may assist this trailing process. Animals grunt and snort, females have a weak mooing contact call and all classes bleat in distress. Like other tragelaphines, males 'click' while courting the female. Gestation lasts about 284 days and the newborn young remains concealed until, with its mother, it joins a nursery group. Sexually mature after 2 years, males are unlikely to mate successfully until they reach their prime at about 4 or 5 years. They live up to 20 years.

ADAPTATIONS Bongos differ from elands in being shorter-legged, shorter-winded and water-dependent, but resemble them in having to range widely in search of concentrated nutritious herbage. They are vulnerable to predators and so stay in, or close to, thick cover where they can hide or defend themselves. Males resemble Nyalas in parading their age and status in strutting displays, but depend less upon visual illusion of mass than real mass. Displays are commonly performed at very close quarters at night.

STATUS Still common in parts of Cameroon, DR Congo and central Africa, the Bongo is in danger of extinction in Sierra Leone and Ghana. It has become rare or vulnerable in Côte d'Ivoire, Gabon and Liberia. The Mountain Bongo has become a 'flagship species' for conservation in Kenya. Conservation plans must take account of its need for unstable habitats. Widespread in moderate numbers and currently not endangered overall. IUCN classifies the species as near-threatened, but the Mountain Bongo *T. e. isaaci* is critically endangered.

GIANT ELAND *Taurotragus derbianus*



Giant Eland

OTHER NAMES Lord Derby's Eland. Fr. *Élan de Derby*. Ger. *Riesenelanantilope*.

MEASUREMENTS HB 2.62–3.20m. T 550–700mm. Sh. ht 1.65–1.78m. W (est. ave.) 450kg (♀), (est. ave.) 900kg (♂).

RECOGNITION A very large bovine with 8–12 vertical white stripes on a sandy grey or rufous body. Both sexes have horns; those of the male are longer (up to 1.23m), more widely splayed and have a looser spiral than in the Common Eland. Mature males also have a black neck and pendulous dewlap from chin to chest. The ears are broad, rounded and prominently marked, as are the hocks.

GEOGRAPHIC VARIATION *T. d. derbianus* (west of R. Niger): rufous, average 15 stripes. *T. d. gigas* (east of R. Niger): sandy-grey, average 12 stripes.

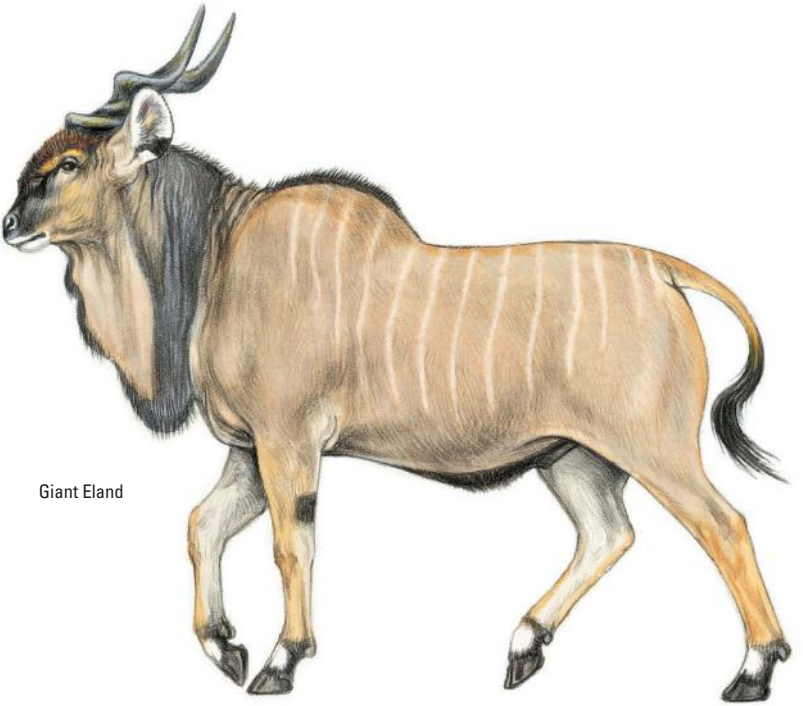
DISTRIBUTION A narrow and increasingly fragmented belt of *Isoberlinia* woodland stretching from Senegal to the Nile and sandwiched between the dry but heavily cultivated wooded savannas of the Sudanian zone and wetter mosaics of forests and grasslands to the south.

HABITAT Quite strictly confined to the *Isoberlinia doka* woodlands where herds (sometimes numbering up to 60) are highly mobile. Occasional vagrants into the wetter savannas to the south of this region have given a misleading impression of the total range. They move long distances to drink but can do without water for some time.

FOOD Browse consists of the dominant leguminous trees, notably *Isoberlinia*, *Julbernardia* and some young grasses and herbs early in the wet season. They will break branches with their horns to get at green leaves.

BEHAVIOUR Highly nomadic, with very large ranges and distinct seasonal movements. Males are often solitary and their contact with females ranges from a few hours to several weeks. Large herds in both wet and dry seasons suggest that security of the young, or social rather than ecological factors, influence female gregariousness. Males have been reported absent from some of these aggregations. Breeding patterns are likely to resemble those of Common Eland or kudus with a 9-month gestation and a brief lying-up period.

ADAPTATIONS Head carriage, horn and dewlap shape and neck colouring suggest that the Giant Eland is intermediate between the 'horn exhibitionist' Greater Kudu and the 'parade bull' Common



Giant Eland

Eland (which displays its body and bulk as a single mass). Both kudus and Giant Elands emphasise height in their strutting displays. Markings serve to focus attention on the head, ears and neck. Of course, large ears are more important for an animal living in thick woodland.

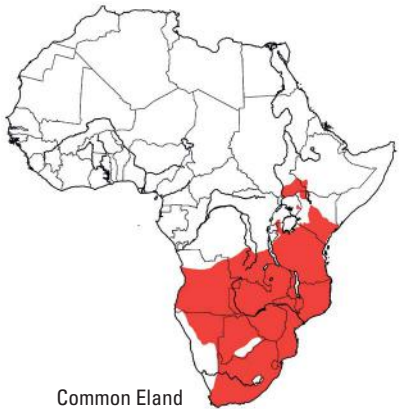
STATUS Giant Elands have been totally or virtually exterminated over a large part of their former range. They remain common in parts of Senegal, Central African Republic, Cameroon and S Sudan, where they are nominally protected in national parks. Their wanderings render them vulnerable to hunting and they are exceptionally susceptible to rinderpest, which hit them very hard in 1983. Listed as threatened (IUCN). Niokola Koba NP in Senegal now supports the only secure population of the western race.

COMMON ELAND *Taurotragus oryx*

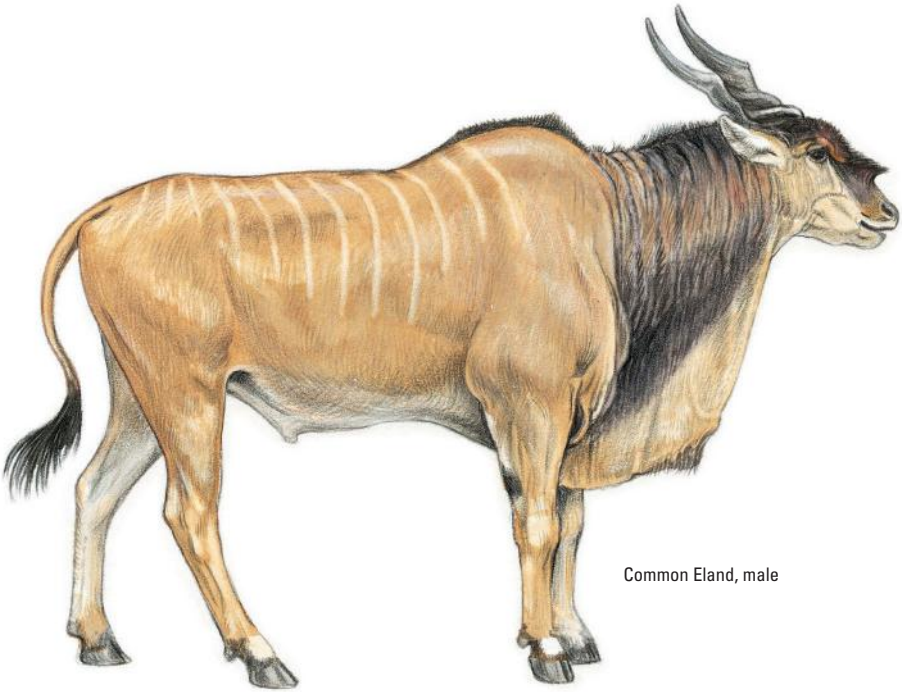
OTHER NAMES Fr. *Élan du Cap*. Ger. *Elanantilope*. Swah. *Pofu*.

MEASUREMENTS HB 2.0–2.8m (♀), 2.4–3.45m (♂). T 500–720mm. Sh. ht 1.25–1.60m (♀), 1.35–1.78cm (♂). W 300–600kg (♀), 400–942kg (♂).

RECOGNITION A very large, tan bovine in which both sexes have horns and a dewlap, a long tail with a tufted tip and narrow, relatively small ears. Males tend to increase in weight throughout their life, neck and shoulders darken from tan to grey and the dewlap enlarges until it hangs like a curtain to below the level of the knees. Hair on the male's forehead also changes with time, becoming more and more bushy (but it can decline in size, suggesting hormonal control). The mouth and muzzle are small and pointed in comparison to those of African



Common Eland



Common Eland, male

Variations in frontal tuft colouring and horn shape of male Common Eland.

Buffalo and cattle. Teeth, jaw muscles and stomach physiology are all adapted to a high-protein, low-fibre diet. The side, or 'false', hooves on the hindlegs are embedded in glandular patches, which presumably leave scent trails.

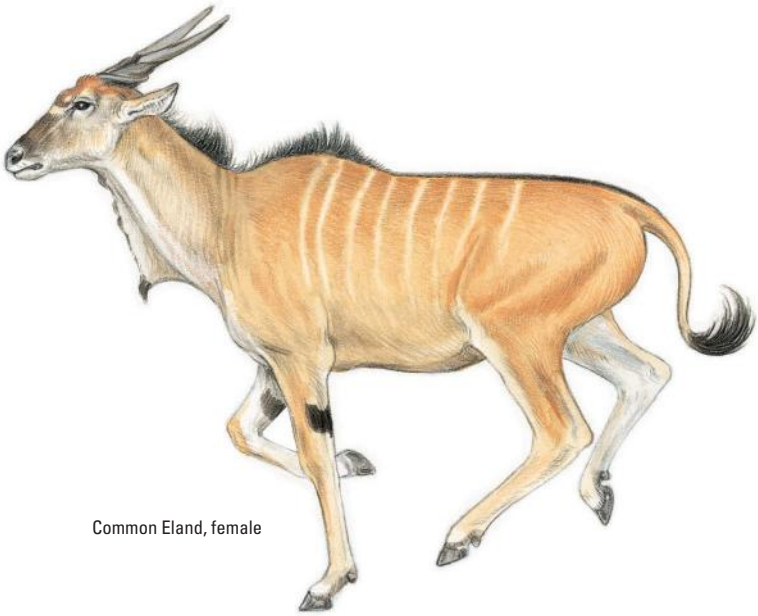
GEOGRAPHIC VARIATION Cape Eland, *T. o. oryx* (S and SW Africa): tawny, adults lose stripes. Livingstone's Eland, *T. o. livingstonii* (central woodlands): brown, up to 12 stripes. East African Eland, *T. o. pattersoni* (E Africa): rufous tinge, up to 12 stripes.

DISTRIBUTION Originally from the Cape to forest margins in the Congo basin, the R. Katonga, to south of the Nile floodplain and arid N Kenya.

HABITAT Primarily animals of the woodlands and woodland–savanna. In South Africa they had extended their range into temperate Highveldt and the Karoo. Common Elands gather into larger herds during and after the rains and scatter into smaller groups in the dry season. For the females this corresponds with a shift into more open country during the rains and into thickets and woodlands in the dry season. Mature males move much less and venture less into the plains. In effect, large female groups form primarily as a defence and for protection of the young.

FOOD Browse consists of foliage and herbs. They can tolerate tougher and more aromatic foods than other tragelaphines. In the dry season, myrrh (*Commiphora*) and bush-willows (*Combretum*) become the major foods in many localities. Marula fruit, acacia seeds and reed syringa (*Burkea*) are other favoured dry-season foods; these are sometimes browsed in poor-quality scrub dominated by *Protea* or hemp (*Diplorhynchus*). Early flushes of grass and herbs attract the elands (notably females more than males). Acacia pods are eaten in quantities during the dry season.

BEHAVIOUR Common Elands are gregarious but have a fluid and open system. Intense mutual attraction among calves leads to temporary isolated groups of up to 50 animals, all juvenile.



Common Eland, female

These calf assemblies provide the nucleus for female herds (in which mothers are to some extent interchangeable). Hierarchies form within these juvenile herds and the principle of 'rank by age and size' remains typical of all ages of these elands and both sexes. The expedient of defensive bunching in open habitats allows independent animals the benefits of herd life without forming ties. Thus no energy is expended seeking lost partners. On the other hand, every animal is alert to local events, such as fires, showers and thunderclouds, thereby causing temporary congregations of up to 1,000 head to form on flushes of green growth. Young animals, especially females, are highly nomadic; older animals, especially males, are more residential. Thus, home-ranges have been found to vary from 1,400 to 1,500km^2. Neighbouring males may be in one another's company with some frequency but seldom number more than six or seven. Larger male assemblies are very temporary and tend to disperse rapidly. More matings have been recorded in the rains, leading to birth peaks nearly 9 months later at the end of the dry season. The young have a brief lying-out period before joining the 'crèches'. Growth rates are exceptionally fast, due in part to the extreme richness of eland milk. In spite of female defence, mortality is high, with predators, disease and accidents all taking their toll. Animals are known to have lived for up to 25 years.

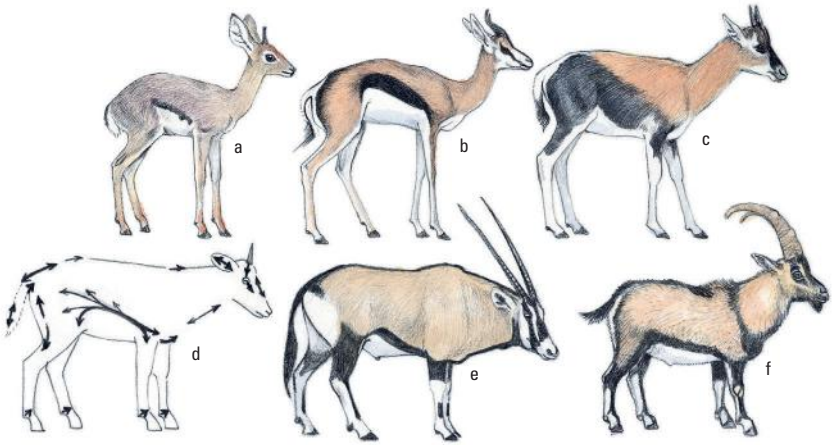
ADAPTATIONS The huge size of males is the most distinctive peculiarity of Common Elands. Continuous enlargement of neck, shoulders, dewlap and facial brush ensures that most of the males within a locality are strung out along a size gradient. This seems to be an extension of the hierarchy formed by very fast-growing calves. The only modification of this strictly linear rank order may be the outbursts of male aggression, known as *ukali*, which may serve as a dispersal mechanism and is typical of most, if not all, tragelaphines.

STATUS Common Elands are hunted over much of their range and have disappeared from most farmed areas. Nonetheless they are still widely distributed and well represented in national parks. They are semi-domesticated as exotics in several countries. Locally vulnerable or endangered (e.g. in Uganda and Rwanda, where, until very recently, they were locally abundant), but overall not endangered.

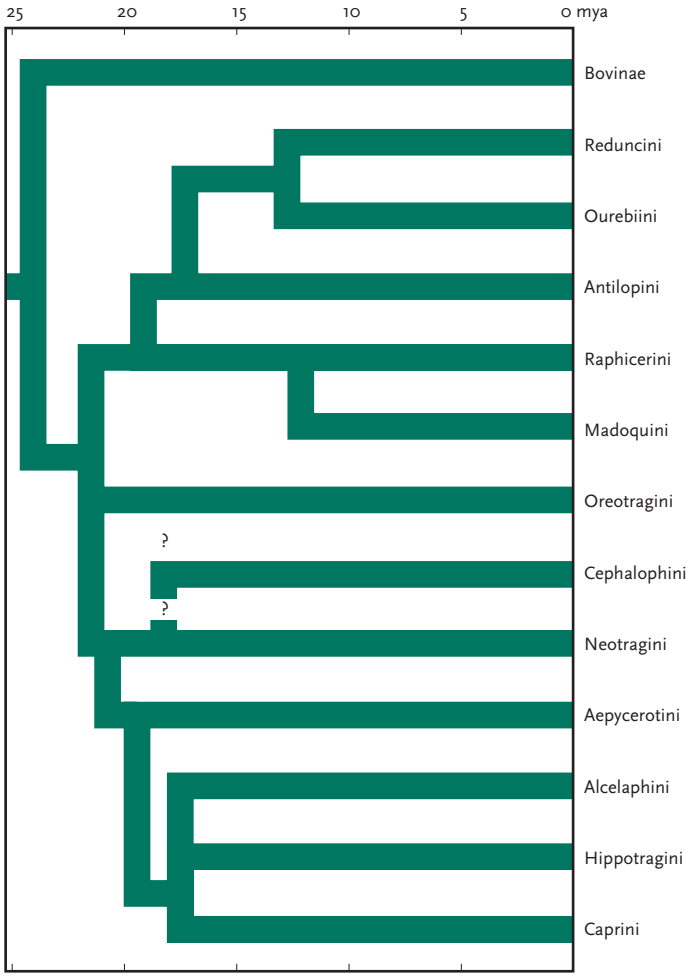
ANTELOPES, SHEEP AND GOATS Antilopinae

Dwarf antelopes	Neotragini
Duikers	Cephalophini
Grysboks	Raphicerini
Dikdiks	Madoquini
Gazelline antelopes	Antilopini
Oribi	Ourebini
Reduncines, kobs	Reduncini
Klipspringer	Oreotragini
Impala	Aepycerotini
Alcelaphines, topi and allies	Alcelaphini
Horse-like antelopes	Hippotragini
Sheep and goats	Caprini

Of all the radiations of animals in Africa, from tree frogs to turacos, guenons to mongooses, the radiation of antelopes is the most celebrated and well known. Ranging in size from less than 2kg to more than 300kg, the very diversity of antelopes typifies them. They began as the newly separate African branch of a common bovid stock some 20–23 mya. A divergence based initially on a separation between bovids on a cooler, mainly temperate, continent and those in a hot, dry, mainly tropical continent selected for opposite traits. Movement between seasonal pastures favoured herding among larger-bodied animals in Eurasia. In Africa, year-round residence on territories favoured spatial intolerance among small-bodied animals. Where the niches of those first pioneers have remained relatively unchanged, small size and territorial behaviour are still favoured, as is evident in dikdiks and other dry-country dwarf antelopes. Whatever morphological changes have taken place over the last 12–18 million years are relatively subtle, thus dikdiks have modified their noses, Klipspringers the structure of their hooves and hairs, while a scarcity of green growth in forest territories selected for shrinkage in the pygmy antelopes. Modest but high-quality diets permitted the early antelopes to live in small territories (some even without water). Recent studies on small, conservative antelopes have shown that home-ranges are generally shared by a pair but marked and defended by the male only. Secretions, notably those from preorbital face glands, are probably just as important for sustaining the cohesion of a pair (or a family) as for land-labelling. Each sex transmits signals that attract the other and the scents, calls and postures of adult females generally provoke the close attention and interest of their male partner several times a day.



Coat patterns in Antilopinae. (a) Beira. (b) Springbok. (c) Bontebok. (d) Diagram of attention-guiding visual foci common to many antelopes. (e) Gemsbok. (f) Goat.



Tentative phylogenetic tree for Bovidae (modified from Hassanin & Douzery 2003, Hernández Fernández & Vrba 2005 and Hassanin *et al.* 2012).

Females show less overt interest in males but are exposed to almost continuous reminders of the male, either by his actual presence or through trails left by his pedal glands, landmarks demarcated by excreta or secretions, or whiffs of scent wafted from the male's sacs, brushes or patches.

Intimate and up-to-date knowledge of a small home-range and its occupants ensures exclusive (and efficient) breeding for both partners. When their offspring are born and inducted into this universe of scents, they too benefit from this shared security.

'Nasal panting', a method of cooling blood in the nose with minimal water loss, is most likely to have begun in small, arid-adapted antelopes because small bodies in hot climates must conserve water and avoid overheating (they cannot afford to waste water through sweating). Being small is therefore functionally linked with this and other conservative habits, such as the possession and use of glands.

Antelopes that do not grow heavier than 16–20kg can survive in territories where exposure to danger is greatly reduced by familiarity with both its food resources and its refuges. They need not enlarge their range, lengthen their legs nor elaborate their horns. This very durable strategy for survival is common, in one form or another, to all small-scale niches. In little modified form, the small antelopes represent descendants from the root stock of all antelopes and present a miniature model for the whole antelope radiation. Thus the dynamics of evolution, the process that has given

us life, are writ large in the living diversity of antelopes, linking their survival with our own (but only when we acknowledge the ancient ecological and continental contexts of our own origins).

A long history of mainly solitary animals attached to defended territories is still evident in a strong bias towards territorial behaviour, even among larger species that have become nomadic. Strong glandular and excretory scents are characteristic of all species. Some glands extrude solid secretions, others disperse aerosols. Horns, often of complex shape, are generally annulated on their forward surfaces, except for a smooth tip (small conservative species sometimes have short, smooth spikes). Noisy gratings of the horns on branches or soil is closely associated with deposition of dung and glandular scents in territorial behaviour. Conspicuously bruised plants help to mark out territory and broadcast scents. Annulated horns assist this function, as well as being able to inflict damage on rivals and trespassers. The evolution of antelope horns has centred on the development of defensive sparring or wrestling and the elaboration of hooks, twists and rams, all of which features are linked with the irregular growth patterns typical of annulated horns.

Their coat patterns are often idiosyncratic but many share a common format that focuses attention on the rump, flanks and head, which suggests a common origin or common mode of elaboration for their patterns. They have various permutations of face, skin and foot glands and, usually, one pair of mammae.

Geographic settings for the very earliest divergences among antelopes can only be guessed at but the equatorial centre–west was clearly the main region of emergence for dwarf antelopes (Neotragini) and duikers (Cephalophini). The south–east realm, instead, was where small antelopes first increased body size, manifest today in the Impala. Klipspringers probably evolved on the Ethiopian massifs and dikdiks in dry piedmonts in north-eastern Africa. Gazelles, horse-like antelopes and proto-caprines probably emerged in North Africa but spread to Eurasia early on. Reduncine reedbuck and lechwe originated in a vast string of flats and wetlands running from Okavango and Zambezia through the L. Victoria basin to the Sudd. Compare the phylogenetic trees on pp.501 and 523 for some current thinking about the antelope radiation.

DWARF ANTELOPES Neotragini

Dwarf antelopes	*Neotragus* (2 species)
Suni	*Nesotragus moschatus*

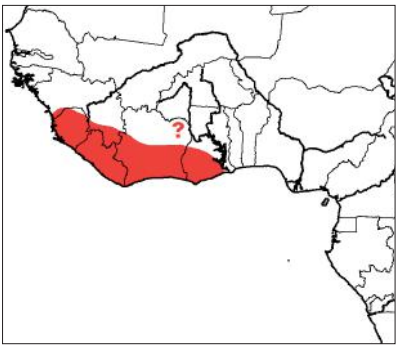
Dwarf antelopes have slender legs, large eyes, a rounded head with a small mouth and muzzle, large preorbital glands and simple spike horns in males. Until recently, and in the first edition of this guide, all small, conservative antelopes were grouped as Neotragini (*sensu lato*). However, molecular genetics has shown that many of these superficially similar little antelopes have long been separate and, in several cases, are linked with the emergence of even more distinctive lineages.

With the Royal Antelope the already small size of conservative species actually declines to an absolute minimum of 1.5kg. *Neotragus* therefore represents dwarfing as an adaptation to living under shade in the equatorial forests of the centre–west. *Nesotragus*, on the other hand, is a larger, and probably older, form occupying the south–east realm where droughts and predation are more frequent. Somehow, the constraints imposed by small size were circumvented by a very early antelope that was more likely to have resembled *Nesotragus* than any other type of small antelope. Once its proportions and body size were free to enlarge, the potential for a much larger, Impala-like antelope became possible.

ROYAL ANTELOPE *Neotragus pygmaeus*

OTHER NAMES Fr. *Antilope royale*. Ger. *Kleinstbockchen*.
MEASUREMENTS HB 380–510mm. T 50–80mm. Sh. ht 240–260mm. W 1.5–3.0kg.
RECOGNITION A tiny antelope with very thin, long legs, a small muzzle, large eyes, relatively small, flesh-coloured ears and a diminutive tail with a white underside. Body colour is reddish or golden brown, with a white belly, chin and chest, and a rufous brown collar. Only males have tiny, conical horns. Its gait is high-stepping under a bunched, compact body but it can slip away in a ground-hugging scamper, or with fast, high jumps powered by disproportionately muscular upper hindlegs.
HABITAT Lives in spaced-out singles or pairs within very small territories, apparently signposted with dung. It prefers dense undergrowth at ground level along forest edges, in clearings, road

Royal Antelope



Royal Antelope

verges and cultivation, both within the moist forest belt and in galleries in drier forest–savanna mosaics. It takes more than a year to mature and can live for 6 years.

FOOD Fresh greenery, buds, leaves, shoots and, less frequently, fruits and fungi. These are plucked with the very small mouth and long tongue. The Royal Antelope feeds during the day but is most often seen by torchlight when it visits verges or farms.

STATUS Still widespread and abundant. Listed by IUCN as not threatened overall but its survival outside parks and reserves could become threatened. It is a major item on West African bushmeat stalls.

DWARF ANTELOPE *Neotragus batesi*

OTHER NAMES Bates's Pygmy Antelope, Bates's Dwarf Antelope. Fr. *Antilope de Bates*. Ger. *Batesbockchen*.

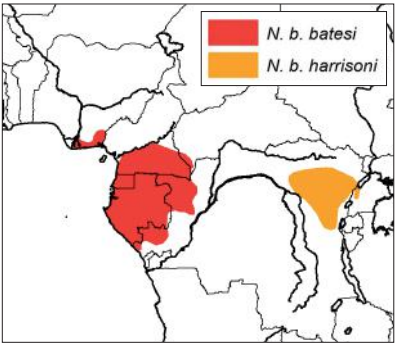
MEASUREMENTS HB 500–575mm. T 45–80mm. Sh. ht 240–330mm. W 2.0–5.5kg (♀ ave. 0.6kg heavier).

RECOGNITION A small, extremely slender-legged, forest antelope with a short muzzle, large eyes and moderately small ears. The soft mahogany-brown fur has a shiny gloss. White markings in the ears and on the chin and throat are conspicuous. The belly is white and the short tail has a lighter underside. The smaller male has very short conical horns.

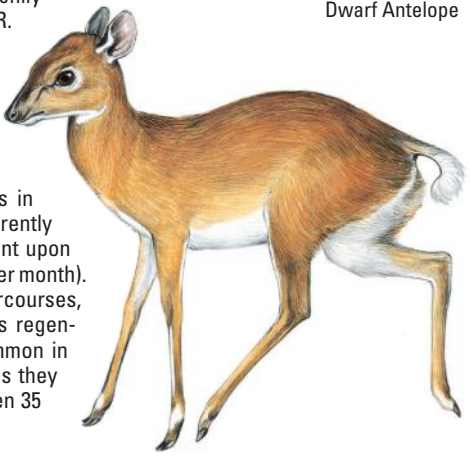
GEOGRAPHIC VARIATION *N. b. batesi* (very patchily distributed between R. Niger and Congo R./R. Sangha), *N. b. harrisoni* (NE DR Congo, W Uganda). A third subspecies might exist in the S Ogooué basin.

DISTRIBUTION Found in discrete pockets in SE Nigeria, parts of SE Cameroon, Gabon and Congo-Brazzaville to R. Sangha. A distinct and equally patchy population occurs in NE DR Congo and W Uganda. They are apparently poor colonists or recolonists and are dependent upon rainfall minima in the dry season (about 50mm per month).

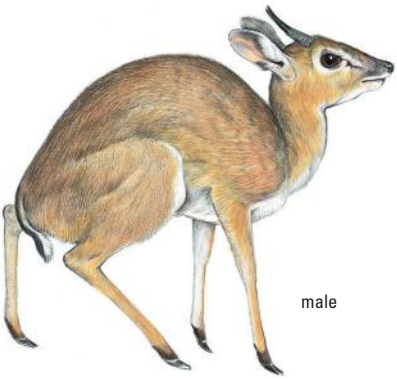
HABITAT Dense, low undergrowth near watercourses, roads, gardens, chablis (tree falls) or in areas regenerating after logging. They are especially common in cocoa plantations. Under favourable conditions they have been known to reach densities of between 35 and 75 per km^2.

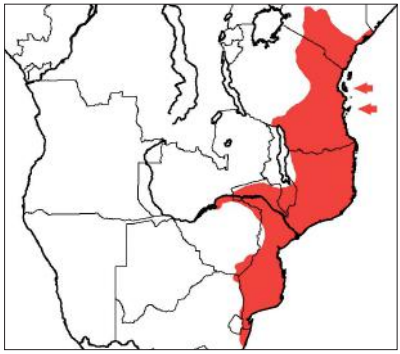


Dwarf Antelope



FOOD A browser of leaves and shoots, rather selective by species and for fresh growth. Recorded preferences are the acanthus *Brillantaisia* and *Phaulopsis*, Bitter Cucumber (*Momordica charantia*) and many cultivars, notably yams, sweet potatoes and peppers.
BEHAVIOUR Males mark their home-ranges with the copious secretions of their facial glands, and torn ears suggest that males fight for territories. They do not seem to make middens, nor to ritualise defecation. Panting raucous barks while fleeing may alert neighbours to a disturbance as well as to the runner's position. Nasal moans are a common contact call. Gestation is thought to be in the region of 6 months, possibly with biannual birth peaks at the end of the rains. Maturation times are not known.
ADAPTATIONS Rapid closure of forest canopies may render this species very dependent on unpredictable tree-fall areas and make its home-ranges less permanent. Periodic rotations of pastures have been observed and greater mobility might explain why overt territorial behaviour is not obvious in this species.
STATUS In spite of its very sporadic occurrence over a vast range, it appears to be common where it is found. It is so marginal as to be very vulnerable in Uganda but is less endangered elsewhere.


male


Suni

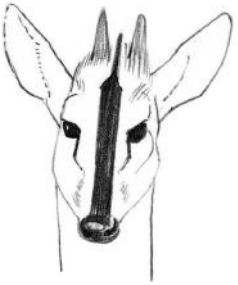
SUNI *Nesotragus moschatus*

OTHER NAMES Fr. *Antilope musquée*. Ger. *Moschusbockchen*. Swah. *Suni, Paa mwekundu*.
MEASUREMENTS HB 570–620mm. T 80–130mm. Sh. ht 300–410mm. W 4–6kg.
RECOGNITION A small antelope with long, slender legs, a typically compact stance and a disproportionately broad head on a short neck. Males have finely annulated horns that reach a maximum of 13mm. The facial glands are enormous, especially in males. The sleek, shiny fur is freckled dark brown with regional and individual differences in the tints of rufous or grey to body colour or legs. The underside is white or very pale grey. The tail has a white underside and is flashed from side to side (rather than flipped up and down, as is the case with the Blue Duiker).
GEOGRAPHIC VARIATION *N. m. moschatus* (N of Zambezi), *N. m. livingstonianus* (S of Zambezi).
DISTRIBUTION A fragmented range from Somalia to Zululand east of the Great Rift Valley.
HABITAT Coastal forests and thickets wherever there is thick undergrowth and regenerating fallow. They are commonest in the broken forests skirting the foothills of large mountain massifs, especially along watercourses, margins and fertile pockets. They have favourite spots within tangles to lie up in. Both visible and invisible scented pathways are regularly followed. Individual and communal dung middens tend to be on the peripheries of a territory.
FOOD Browsers with a varied diet of leaves, shoots and herbs and, more rarely, grass, roots and mushrooms. Among the commonest food plants are Sunn Hemp (*Crotalaria juncea*), *Commelina*, *Acacia* and brandybush (*Grewia*), which are all eaten off the plant. Sunis prefer false nettles (*Fleurya*) and morning glories (*Ipomoea*) that are wilted and pick up various dry fallen leaves. They gather under feeding colobus monkeys to pick up dropped leaves and shoots of brittlewood (*Nuxia*). They feed in short bursts interspersed with rests and are most active after rainstorms or spells of dense mist, especially between nightfall and 22.00 and after 04.00. They rest during the heat of the day.

BEHAVIOUR Mainly pairs on territories of approximately 3ha. Where larger numbers of females (up to four) share a male home-range he associates more closely with just one female. Incursions into territories by other males are met with energetic grating of the horns and chases in which the aggressor champs his jaws while trying to strike glancing blows or parry horn jabs. A higher ratio of females in most populations is probably due to deaths following the fierce contests of territorial males. Males do not acquire full adult characteristics before 14 months of age but females are thought able to breed by about 6 months. One, very rarely two, young are born after a gestation of 180 days. There is a birth peak just before the rains in February–March. Young keep hidden and make a soft, bird-like contact call that resembles grating marbles. They begin browsing within days of birth and the suckling period is very brief. Animals are known to live for at least 6 years.
ADAPTATIONS Well named the 'musk antelope', the Suni has a strong body odour (in addition to more specific preorbital and pedal gland scents). These smells demarcate territory and identify the sex and status of individuals, but also appear to act as insect repellants.
STATUS Although very localised in an environment subject to much depletion (for wood, charcoal and farmland), Sunis remain common and widespread through parts of their total range. Sold in bushmeat markets (sometimes deliberately maimed), they are subjected to unconscionable cruelty.

DUIKERS Cephalophini

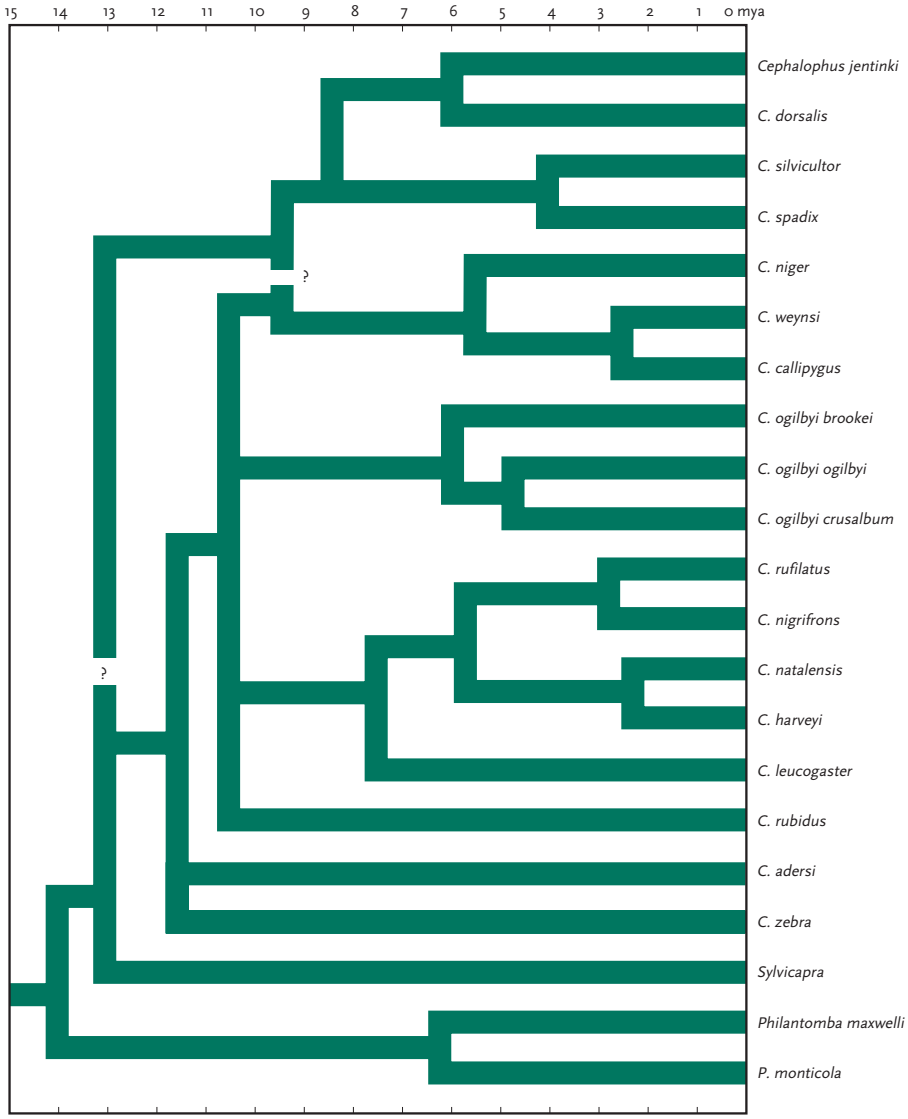
Blue duikers	*Philantomba* (3 species)
Bush Duiker	*Sylvicapra grimmia*
Forest duikers	*Cephalophus* (16 species)



Bush duiker

Black-fronted Duiker

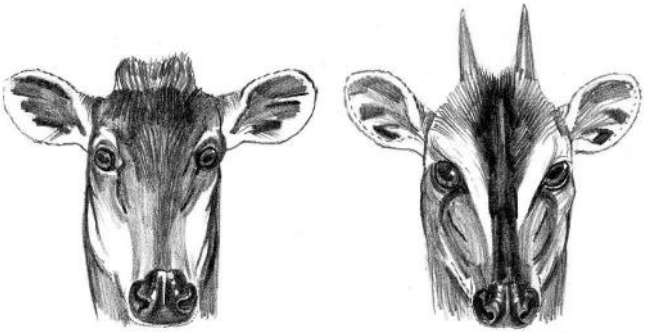
RECOGNITION Duikers are antelopes with a compact body and a short, wedge-shaped head, with horns normal for both sexes (except female bush duikers). The mouth is large, with a wide maw. All species have 'smear-type' facial glands on the sides of their muzzle; some have glands in the groin, under tufts of hair on the legs or between the hooves. They range in size from 3.5 to 80kg. Legs vary in length from species to species but none can compare with open-country, running antelopes. Intensely territorial, the males of most species can be called up by imitating the duiker's bleat.
GENEALOGY Duikers follow a broad progression in which the smallest belong to more conservative lineages while the largest are the more advanced. Dwarfing is one mechanism whereby leaf-eating herbivores can first adapt to the scarcity of herbage on the forest floor. Only after initial dwarfing could the ancestral duikers make a dietary reversal back to more frugivorous, even omnivorous, diets. Duikers are rare in the fossil record. However, their brain morphology is consistent with their being advanced derivatives of the dwarf antelopes. They have among the largest and most complex brains of all bovids.
GEOGRAPHY Most duikers live only in forest but some have adapted to more open, swampy or montane environments. They are exclusively African and there are no fossils to suggest they ever crossed the Sahara.
ECOLOGY The ecological partitioning of forest duikers is summarised later (see p.534). The duiker radiation involves isolation, regional specialisation, partitioning of the habitat by food type, by



Phylogenetic tree for Cephalophini (adapted from Jansen van Vuuren & Robinson 2001 and Hassanin *et al.* 2012).

activity (diurnal, nocturnal) and, above all, size differences. All duikers are to a greater or lesser extent dependent upon monkeys, squirrels, birds and fruit bats to dislodge the fruits, flowers and leaves on which they feed. Part of their alertness and 'strategic intelligence' is linked with this sensitivity to what is happening in the canopy. Some duikers can clamber up sloping trunks or dense tangles, some are specialised in skilled concealment (mostly during the day), relying on a short fast dash to escape if found. All can make prodigious leaps when pursued.

NATURAL HISTORY All species are thought to be territorial and most form close associations between the sexes, each excluding others of their own sex. The size of territories and degree of exclusivity (particularly along margins) probably varies greatly. Well-trodden paths connect habitual feeding,



Bay Duiker (*right*), Yellow-backed Duiker (*left*) to show former's larger eyes, broader face and shorter muzzle.

ruminating, sleeping and refuge areas. All species use scents and vocalisations to regulate social contacts. Precocious young are born after a relatively long gestation. All are slow to reach full maturity, suggesting that prolonged learning may be necessary for successful exploitation of a difficult environment.

ADAPTATIONS Duikers have thickened and enlarged frontal bones and their short, sometimes vestigial, horns grow from further back on the skull than in other antelopes. This can be correlated with hard head-butting in many species, directed at rivals and (less commonly) predators, hard fruits and crashing through undergrowth. Their reduced horns and other neotenous features are further indications of dwarfed origins.

The tentative phylogenetic tree opposite summarises current knowledge of duiker relationships.

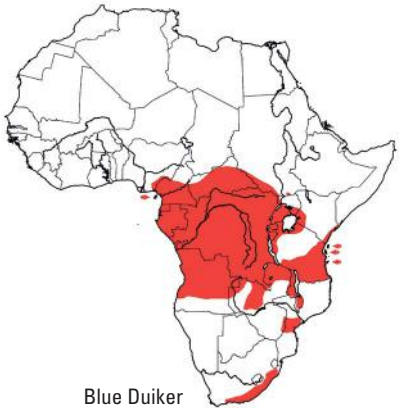
BLUE DUIKERS *Philantomba*

Blue Duiker	*Philantomba monticola*
Maxwell's Duiker	*Philantomba maxwelli*
Walter's Duiker	*Philantomba walteri*

Blue duikers are small, greyish, brown or fawn animals that have retained many of the original adaptive traits of the duiker tribe but clearly refined their own niche at an early date. Formerly considered to be two species, but a third is profiled here. *P. monticola* occupies a wide range in central and southern Africa, and breaks down into two major divisions (N and S of the Congo R.). *P. maxwelli* occurs in West Africa and its easternmost population (in the Dahomey Gap) has recently been described as a third, previously overlooked species, *P. walteri*. Blue duikers have become a very successful and widely distributed group.

Philantomba spp. frontal views of Maxwell's Duiker (*left*); Blue Duiker *P. monticola congicus* (*centre*); and Blue Duiker *P. m. monticola* (*right*). Several current subspecies may well prove to be full species.

BLUE DUIKER *Philantomba monticola*

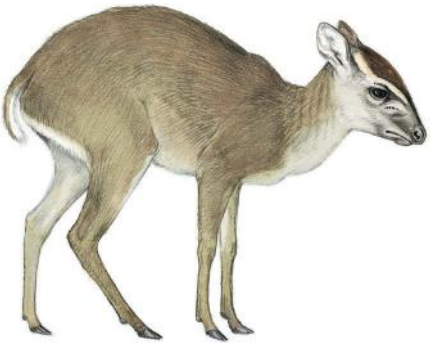

Blue Duiker

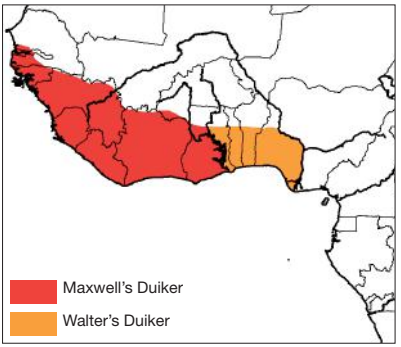
OTHER NAMES Fr. *Céphalophe bleu*. Ger. *Blauducker*. Swah. *Ndimba, Chesi*.
MEASUREMENTS HB 550–900mm. T 70–130mm. Sh. ht 320–410mm. W 3.5–9.0kg.
RECOGNITION A small, grey or brown antelope that has differentiated into a large number of regional and insular species. Populations living in very wet areas tend to be much darker than those in drier areas. It has large eyes, rather small ears and a very wide, flexible mouth. The tail has a narrow midline of black but the underside and fringe has white, crinkled hairs that reflect light so well that the flickering tail resembles a small flashlight going on and off along the dark forest floor.
GEOGRAPHIC VARIATION 26 subspecies named. Two main divisions. Also montane and insular races.
South–east division – russet legs: *P. m. monticola* (southern Africa, eastern littoral), *P. m.bicolor* (KwaZulu to R. Zambezi), *P. m. hecki* (east coast littoral), *P. m. defriesi* (central Africa), *P. m. anchietae* (Angola), *P. m. simpsoni* (S Congo basin).
Centre–west division – grey legs: *P. m. congicus* (Cross R. to Congo R.), *P. m. aequatorialis* (R. Uelle to W Kenya).
Dark montane isolates: *P. m. lugens* (southern highlands, Tanzania), *P. m. schusteri* (Eastern Arc Mts, Tanzania), *P. m. fuscicolor* (Manica highlands).
Insular forms: *P. m. sundevalli* (Zanzibar I.), *P. m. pembae* (Pemba I.), *P. m. melanorheus* (Bioko I.).
DISTRIBUTION Forest and forest mosaics from the R. Niger to W Kenya, and from Angola to the east coast (Cape to R. Tana).
HABITAT Lowland and montane rainforests, riverine and littoral forests and moist thickets. Patchily distributed and at variable densities because of its dependence upon a year-round supply of fruits. The animals normally rest all night, under cover from rain or beside tree trunks. In disturbed areas they may become more nocturnal.
FOOD Where fruiting trees and shrubs are abundant, up to 80% of the diet may be fruits, otherwise foliage with traces of flowers, gum and animal matter is taken. Preferred fruits are the abundant small berries or seeds that are often typical of dominant trees in secondary or colonising forest. Dry fallen leaves are commonly eaten. Blue Duikers have been seen to follow below monkeys and birds to pick up fallen fruits.
BEHAVIOUR Bonded pairs are formed on a small and regularly traversed territory (as little as 2.5–4.0ha in rich W African forests). Such territories are saturated with scent clues emanating from a continuous flow from pedal glands (between the hooves), frequent rubbings from the face glands, and from faeces, urine and horn-gratings. Both sexes chase off intruding duikers but tolerate their own offspring for up to 18 months. Forays outside the territory are made to temporary food sources (and by the male while the female has her newborn lying-up). Gestation has been reported as 5 months, but 4 months is a more likely estimate. The mother and young make contact through soft, groaning calls and both freeze at the slightest alarm, only running if encountered unexpectedly. At such times a male may

utter a whistle or sneezing call that both signifies alarm and advertises movement and position to its mate and neighbours. Young mature slowly (i.e. 2 years) and are known to live for 10 years.

ADAPTATIONS Densities of up to 62–78 per km^2 have been recorded in the fruit-rich forests of Gabon. This implies that this species is particularly efficient at picking up the ephemeral resources that fall from the trees above. It is very likely that such densities are only possible where there are very large numbers of monkeys and birds displacing and 'wasting' a super-abundant fruit supply. Close bonding of a pair may assist this strategy by reducing danger from predators and increasing the thoroughness with which the ground is covered.

STATUS In spite of heavy hunting pressure all over its range, this duiker is still widespread and common. However, felling of fruit trees and killing of monkeys degrades their habitat and food supply.





Maxwell's and Walter's Duikers

MAXWELL'S DUIKER *Philantomba maxwelli*

OTHER NAMES Fr. *Céphalophe de Maxwell*. Ger. *Maxwellducker*.

MEASUREMENTS HB 630–760mm. T 120–150mm. Sh. ht 350–420mm. W 6–10kg.

RECOGNITION The Upper Guinea counterpart of the Blue Duiker, distinguished by its strongly marked and more angular head, clearly demarcated facial glands and deeply pocketed pedal glands. It is grey-brown with paler neck, chest and undersides but without white markings. Both sexes are normally horned but some females lack horns.

GEOGRAPHIC VARIATION Six named subspecies (two from mid-river islands).

DISTRIBUTION Intermittently from Senegal to the Dahomey Gap.

HABITAT Rainforest galleries and relicts, in moist or derived savannas with abundant fruiting trees and shrubs.

FOOD Fallen fruits, herbs, shrubs and new growth; probably some animal matter.

BEHAVIOUR Generally resembles the Blue Duiker, i.e. pairs share a small common territory defended against others of the same sex. The territory is incidentally marked by the pedal glands, faeces and urine, more deliberately marked with facial glands. Gestation is reported to be 120 days. The young of captive specimens maintain tranquil relations with parents for more than a year. They are fully mature by 2 years.

ADAPTATIONS Face glands are used to mark not only surroundings but also companions within the territory. Both sexes mark and both also solicit and receive grooming, in which face, ears and neck are licked vigorously. Gestures of appeasement are also linked with face-licking and suggest that close family bonds are continually maintained.

STATUS Maxwell's Duiker has lost much habitat and is hunted intensively, often excessively. In spite of this it is still widespread and common.

WALTER'S DUIKER *Philantomba walteri* (not illustrated)

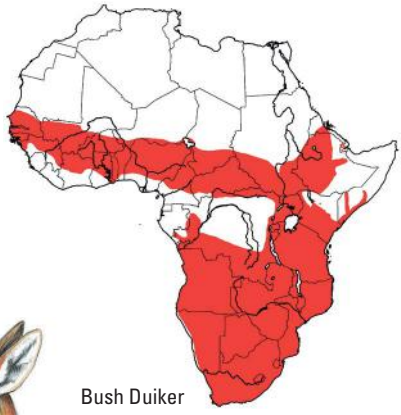
OTHER NAMES Fr. *Céphalophe de Walter*. Ger. *Walterducker*.

MEASUREMENTS No data. Likely to be slightly smaller than Maxwell's Duiker.

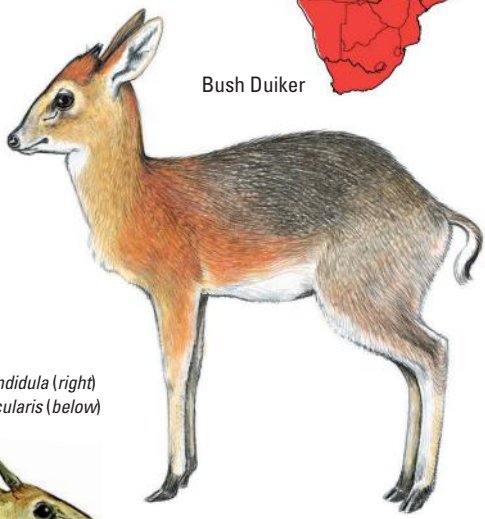
RECOGNITION Newly described species based on morphology and genetic data. Formerly considered to be the easternmost population of Maxwell's Duiker. Intermediate in size between the larger Maxwell's Duiker to the west and the smaller Blue Duiker to the east. Morphologically

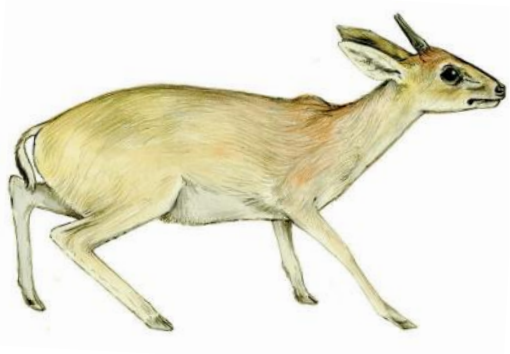
similar to Maxwell's Duiker with a relatively long tail, large pedal glands and striking superciliary line, but differs from the other two species in the genus in cranial measurements, having a smaller nasal constriction and cranial height.
GEOGRAPHIC VARIATION None known.
DISTRIBUTION Occurs from the Dahomey Gap (Togo and Benin) to the R. Niger in Nigeria.
HABITAT As Maxwell's Duiker.
FOOD Presumably similar to other species in the genus.
BEHAVIOUR Presumably as Maxwell's Duiker.
STATUS Populations in Togo and Nigeria are considered to be vulnerable and those in Benin are probably threatened. The species is clearly at risk from deforestation and considerable hunting pressure – the first specimens of this new taxon, which led to recognition of its distinctness, were discovered in a bushmeat market.

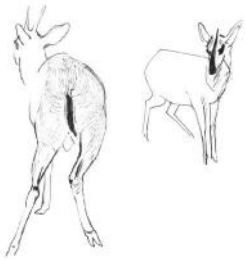
BUSH DUIKER *Sylvicapra grimmia*


Bush Duiker

OTHER NAMES Common Duiker, Grey Duiker, Grimm's Duiker. Fr. *Céphalophe couronné*. Ger. *Knonenducker*. Swah. *Nsya*.
MEASUREMENTS HB 900–1,115mm (♀), 700–1,050mm (♂). T 70–195mm. Sh. ht 450–700mm. W 10.0–22.4kg (♀), 10–26kg (♂).
RECOGNITION The long but typical duiker face has swollen face glands and a black facial midline, ending in a rounded, leathery black nose. The Bush Duiker is longer legged and larger eared than the forest duikers. Colouring varies from region to region, with plain tawny animals in the far east and west and heavily grizzled, grey or brown animals in the central part of its range. The short tail is black above, white below. Straight, upright horns, only in the male, measure up to 180mm.
GEOGRAPHIC VARIATION More than 40 races listed but regional groupings can be recognised: *S. g. grimmia* group (S Africa); *S. g. steinhardti* group (Kalahari region); *S. g. orbicularis* group (E Africa); *S. g. splendidula* group (S Congo basin); *S.*


S. g. splendidula (*right*)
S. g. orbicularis (*below*)





g. rosevelti group (Niger to Nile savannas); *S. g. abyssinica* group (Uganda to Eritrea); *S. g. deserti* (Somali–Kenya littoral); *S. g. coronata* (Upper Guinea savannas). They are darker in moist habitats and lighter in drier habitats.

DISTRIBUTION Savannas and woodlands of sub-Saharan Africa. They are absent from forests, open plains, deserts and subdeserts but live in various mountain areas up to the coldest alpine zones.

HABITAT They flourish in a wide range of habitats where their need for shelter and suitable food can be met. They benefit from reduced predation and patches of low secondary growth in settled areas, including suburbia. They avoid the heat of the day and also rest up for a large part of the night.

FOOD Leaves and shoots of numerous dominant bush plants, such as *Acacia*, bush-willow (*Combretum*), myrobalan (*Terminalia*) and morning glories (*Ipomoea*). Fruits are also very important seasonally, notably the pods of leguminous trees and shrubs, figs and the fruit of the Duiker Tree (*Sapium integerrimum*) and Kudu Berry (*Pseudolachnostylis maprouneifolia*). Flowers, bark, resin, roots, bulbs, tubers and fungi are also eaten; also traces of grass. Animal foods are rarer but not infrequent. Bush Duikers do not need water.

BEHAVIOUR Males defend territories with little or no overlap in range. Female home-ranges are also discrete but may be based more on avoidance. Male territories can enclose more than one female range. Lying up is solitary and females prefer lower, denser refuges while males select higher, more open vantage points at which to rest or ruminate. Both sexes are active during courtship, with much chasing and play. Gestation is thought to last about 6 months. The young lie up in dense cover for several weeks and mature very rapidly. Reaching near adult size in 6 months, some females drop their first calf at 1 year of age. They live for at least 12 years.

ADAPTATIONS In spite of being hornless, females are larger than males and capable of butting both other duikers and small predators approaching the young. Juveniles bleat very loudly if caught and both parents converge at once. This behaviour is exploited by hunters who imitate the bleat to call duikers within range.

STATUS Still widespread and common.

FOREST DUIKERS *Cephalophus*

Zebra Duiker	*Cephalophus zebra*
Aders's Duiker	*Cephalophus adersi*
Rwenzori Red Duiker	*Cephalophus rubidus*
White-bellied Duiker	*Cephalophus leucogaster*
Natal Red Duiker	*Cephalophus natalensis*
Harvey's Duiker	*Cephalophus harveyi*
Red-flanked Duiker	*Cephalophus rufilatus*
Black-fronted Duiker	*Cephalophus nigrifrons*
Ogilby's Duiker	*Cephalophus ogilbyi*
Weyns's Duiker	*Cephalophus weynsi*
Peters's Duiker	*Cephalophus callipygus*
Black Duiker	*Cephalophus niger*
Abbott's Duiker	*Cephalophus spadix*
Yellow-backed Duiker	*Cephalophus silvicultor*
Bay Duiker	*Cephalophus dorsalis*
Jentink's Duiker	*Cephalophus jentinki*

There are at least 16 species of forest duikers and one or more of them once occupied virtually every type of forest in Africa. Supposed relationships within this enormous radiation are summarised in the tentative phylogenetic tree on p.528.

Cephalophus is the most diverse duiker group. The smaller ones are conservatives, occupying peripheries or islands that are marginal to their central habitat – equatorial forest. The Zebra Duiker, *C. zebra*, would seem to derive from the earliest beginnings of this radiation. Genetically, its closest affinities are with Aders's Duiker, *C. adersi*, a relict 'dwarf red' confined to coral rag and other coastal forests along the Kenya/Tanzania coast and to Zanzibar I. The Rwenzori Red Duiker,

Forest type	Lowland forest: closed, high canopy, thin undergrowth	Lowland and montane forest: broken canopy, dense undergrowth	Alpine and subalpine habitats	Swamp forest	Gallery, riverine and drier, low-canopy forests	Forest edge and secondary growth
Main food resources for duikers in possible order of importance	Fruit, shoots and seedlings, leaves, flowers, bark and fungi	Fruit and herbaceous growth, leaves, shoots and seedlings, fungi	Herbaceous growth, leaves, fruit, moss, young grass	Fruit, herbaceous growth, fungi, bark, semi-aquatic vegetation	Fruit, leaves, seasonal shoots, seedlings and herbaceous growth	Fruit, herbaceous growth, shoots and seedlings
Species (*Cephalophus* and *Philantomba*)						
C. silvicultor 68 (45–80)kg	mainly nocturnal (in Gabon 71% fruit, 29% leaves)					
C. spadix 55 (52–60)kg		allopatric sibling sp. of above (montane only)				
C. dorsalis 22 (14.5–24)kg	nocturnal (in Gabon 73% fruit, 27% leaves)					
C. callipygus 20 (16–23)kg	diurnal (in Gabon 83% fruit, 16% leaves)					
C. nigrifrons 17 (13–18)kg		diurnal (in Gabon 72% fruit, 28% leaves)				
C. harveyi 15 (13–16)kg		diurnal and nocturnal			diurnal and nocturnal	
C. rubidus 15kg			diurnal			
C. leucogaster 13 (12–18)kg		in Gabon 73% fruit, 27% leaves and flowers			diurnal	
C. rufilatus 13 (12–14)kg					diurnal and nocturnal	
C. natalensis 13 (12–14)kg					diurnal and nocturnal	
C. adersi 8 (6.5–12)kg					diurnal	
P. monticola 5 (3.5–9)kg	in Gabon 78% fruit, 20% leaves				mainly diurnal	

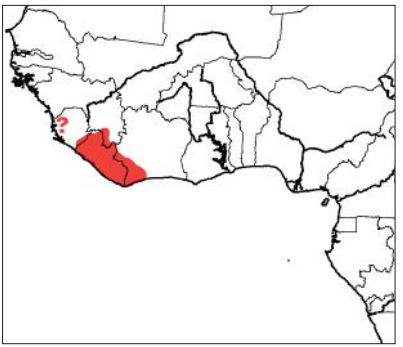
Food and habitats of duikers (dietary data from Gautier-Hion, Emmons and Dubost 1980).

C. rubidus, lives at the highest altitudes on the very wet, cold Rwenzori Mts. (On drier peaks the Bush Duiker, *Sylvicapra*, has moved into this niche.) The White-bellied Duiker, *C. leucogaster*, seems to derive from an earlier population that has only survived competition with its near-descendants by becoming a semi-nomadic inhabitant of mono-dominant zones such as Limbali (*Gilbertiodendron*) forests. It belongs to a branch of adaptable species that includes the Natal Red and Harvey's Duikers, *C. natalensis* and *C. harveyi*, generalised south–eastern duikers. Two other members of this branch have adapted to marginal environments within the forest. The Black-fronted Duiker, *C. nigrifrons*, has become a swamp specialist while the Red-flanked Duiker, *C. rufilatus*, is a small, generalist in literally 'marginal' habitats along the northern edges of the rainforest belt.

The prime forest niche for medium-sized duikers living in territories and feeding on rich nutritious foods such as fallen fruits is occupied by 4–6 species, three of which are recently evolved (*C. weynsi*, *C. callipygus* and *C. niger*) and appear to be in the process of replacing their precursors (*C. ogilbyi* group). Sharing the smooth, short neck hair, robust, long skull and broad noses that typify the 'giant' Black Duiker, *C. niger*, there is some uncertainty as to whether the giant duikers emerged out of this lineage or share common origins with *Silvicapra*.

The origins of two so-called 'fibre duikers', *C. dorsalis* and *C. jentinki*, are equally uncertain but they probably originated in Upper Guinea, where they are mainly confined to primary rainforest. The widely distributed Bay Duiker, *C. dorsalis*, is the most advanced in its adaption to hard, fibrous foods. Molecular clocks have suggested that the *Cephalophus* radiation has taken place within the last 14 million years and in response to repeated fragmentation of forest blocs as climates fluctuated. This helps to explain the survival of relict or specialised forms in marginal or isolated localities.

ZEBRA DUIKER *Cephalophus zebra*



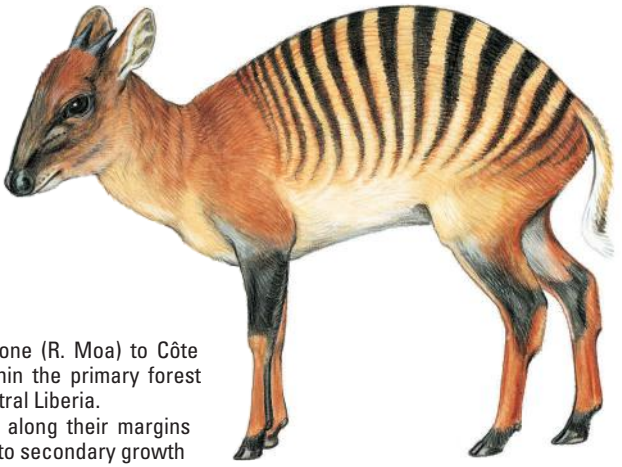
Zebra Duiker

OTHER NAMES Banded Duiker. Fr. *Céphalophe zébré*. Ger. *Zebraducker*.

MEASUREMENTS HB 700–900mm. T 100–150mm. Sh. ht 400–500mm. W 15–20kg.

RECOGNITION As its name suggests this duiker has a panel of vertical, vivid black-and-cream stripes from behind the shoulder to the tail. The head, shoulders and lower legs are russet red, with hocks, muzzle and leg joints nearly black. Both sexes have robust, conical and very sharply pointed horns above a forehead and nasal area where the bone is massively thick and reinforced. They have prominent tufted glands just below the heels of the back legs and glandular pockets in the groin.

GEOGRAPHIC VARIATION None. Alternative and now obsolete scientific names are: *C. zebrata*, *C. doria* and *C. doriae*.



DISTRIBUTION From Sierra Leone (R. Moa) to Côte d'Ivoire (R. Niouniourou) within the primary forest zone. Commonest in east-central Liberia.

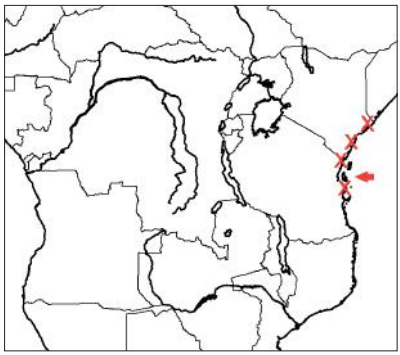
HABITAT Primary forests and along their margins and in clearings, extending into secondary growth and swidden cultivation. It favours lowland forest (notably the Sinoe and other river valleys in Liberia) but may also live in low montane and hill forests.

FOOD Fruits and foliage. Details are unknown but the Zebra Duiker does not appear to have specialised teeth or diet. It may use its head to break open the shells of larger fruits.

BEHAVIOUR Friendly relations between captive pairs involve mutual rubbing and licking, suggesting that breeding pairs are the normal social unit (as they are in most duikers). Because both sexes have horns and a thickened skull (which do not appear to correlate with a specialisation in ecology or diet), it seems likely that bonded pairs share defence of their home-range against intruding duikers. Scarred heads suggest that the collisions that are normal in duiker confrontations are particularly vigorous and uninhibited in these exceptionally stocky and muscular antelopes.

ADAPTATIONS Known to be a strong stimulus to the eye/brain sensory system, stripes may serve as a focus for social attraction (in which case the resemblance of these duikers to zebras may be more than superficial). An advantage of stripes in this species could be to inhibit goring of the soft abdomen during aggressive encounters. Thus, while other animals shield themselves from the worst effects of aggressive rivalry with thickened skin, bony plates, etc., these duikers may have a subtler strategy for reducing damage during excessive aggression.

STATUS Formerly widespread over much of Liberia and Sierra Leone, Zebra Duikers are declining fast as their habitat is being destroyed and commercial bushmeat hunting becomes more entrenched and appallingly comprehensive in its onslaughts. Listed as threatened (IUCN) in Liberia but in danger of extinction in Sierra Leone and Côte d'Ivoire.

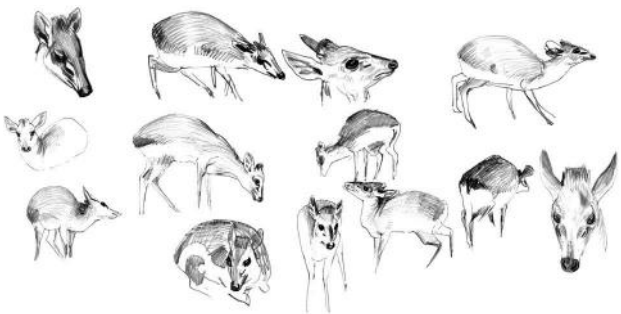


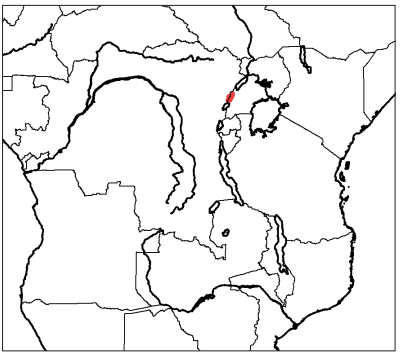
Aders's Duiker

ADERS'S DUIKER *Cephalophus adersi*

OTHER NAMES Fr. *Céphalophe d'Aders*. Ger. *Adersducker*. Swah. *Paa nunga*.
MEASUREMENTS HB 660–720mm. T 90–120mm. Sh. ht 300–320mm. W 6.5–12kg.
RECOGNITION A small duiker of a washed-out, tawny-red ground colour with a bold white band across the buttocks and white freckling on the red legs. The neck is greyish and there is a red tufted crest. Fur is particularly soft and silky. The muzzle is pointed, with a rather flat front to the nose.
HABITAT In Zanzibar this species has become almost entirely restricted to tall thicket forest growing on waterless coral rag. Its survival is influenced by all the commonest trees and shrubs bearing prolific crops of flowers and berries. Dominant tree species are Ebony (*Diospyros consolataei*), Kooboo-berry (*Cassine aethiopica*) and Bush Guarri (*Euclea schimperi*), with an understorey of turkey berries (*Canthium* spp.) and *Polyspheria*.

Pairs live in territories and breed throughout the year. They feed from dawn to about 11.00, after which they rest and ruminate before becoming active again from 15.00 to nightfall. Aders's Duiker is extremely alert and sensitive to sound so that driving with nets and dogs or silent ambush at a feeding tree are the main methods of hunting it.
FOOD Fallen flowers, fruits and leaves, often picked up beneath foraging monkeys and birds; also sprouts, buds and fresh growth.
STATUS In danger of extinction along the Kenya and Tanzania coasts, the main hope for this duiker's survival lies in Zanzibar (Nguja) I., but this requires the declaration and protection of national parks. Regulation of hunting, formerly exerted by both central administration and by village elders, has been scrapped since the 1962 revolution and local hunters describe a reduction in their harvest of antelopes of 20–30% in recent years. This may be partly due to felling and charcoal-burning in the remaining areas of tall coral thicket. Hunters will travel as far as 30km on foot in order to obtain duikers from well-known 'hot spots', such as Michamvi and Mamboiya. At Mtende Aders's Duiker has been estimated to form 70% of the hunters' antelope kills. As its habitat becomes more fragmented, free-ranging or feral dogs become a major menace. Dogs are known to have eliminated the entire population of Aders's Duikers on Funzi I. (where it had been reintroduced and flourished). Listed as threatened (IUCN).





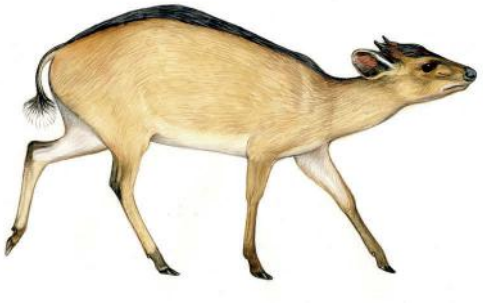
Rwenzori Red Duiker

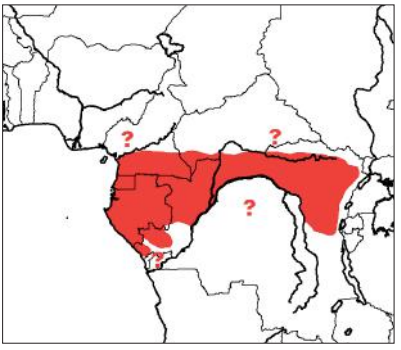
RWENZORI RED DUIKER *Cephalophus rubidus*

OTHER NAMES Fr. *Céphalophe du Ruwenzori*. Ger. *Ruwezoriducker*. Konjo dialect *Isuku*.
MEASUREMENTS HB 750mm. T (ave.) 100mm. Sh. ht (ave.) 450mm. W (est.) 15kg.
RECOGNITION A stocky duiker with a dense, glossy rufous coat with long, coarse hair on the neck, changing to dense, soft fur over the hindquarters. The belly is white, hindlegs are almost black and there are dark-brown markings on the joints of the forelegs. A black or dark-brown blaze stretches from the nose to the crown. Down the midline of the back and neck there is a zone of dark grey underlying the uniform red tips of the fur. The underfur of the flanks is cream.
GEOGRAPHIC VARIATION The lower slopes of the Rwenzori Mts are inhabited by a race of the Black-fronted Duiker, which has a thinner, harsher, grizzled coat. Nonetheless, it is possible that the two are actively hybridising in a region of overlap at about 3,000m.
HABITAT Afroalpine and subalpine zones, *Hagenia* woodland and bamboo zones of Rwenzori.
FOOD Browse in a rich and continuous pasture of herbs, notably wild parsleys, balsams, violets, sorrels and *Galium*, a scrambling herb much favoured by all high-altitude herbivores. The Rwenzori Red Duiker is mainly diurnal but activity periods could be strongly influenced by rain.
STATUS Heavily snared. Climbers have reported a substantial decline or disappearance along the Bujuku and Kitandara routes to the peaks. Vulnerable.

WHITE-BELLIED DUIKER *Cephalophus leucogaster*

OTHER NAMES Fr. *Céphalophe à ventre blanc*. Ger. *Weissbauchducker*.
MEASUREMENTS HB 780–1,000mm. T 80–150mm. Sh. ht 420–510mm. W 15–20kg.
RECOGNITION A pale forest duiker with warm, sandy-brown forequarters, graduating towards grey near the black dorsal line. The rump has a rufous flush and the crest is orange. The front, heels and hocks are black. The underside is white. The nape is short-furred but the rest of the neck has long,





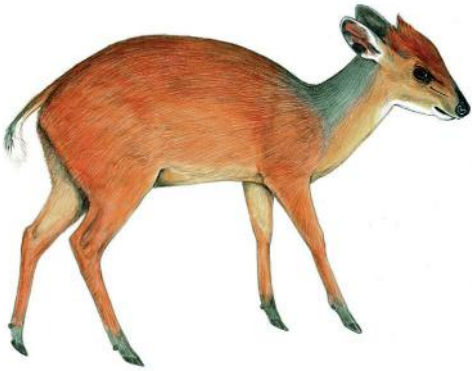
White-bellied Duiker

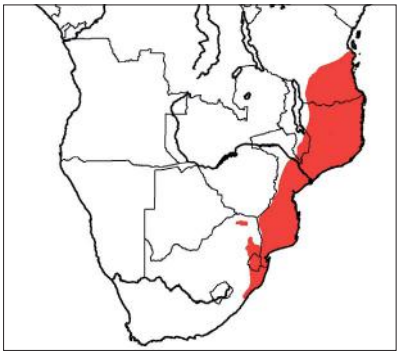
coarse hair. The tail has a fluffy, black-and-white tip. It appears to have a deeper jaw, a wider gape and a stronger bite than other duikers with coarse neck fur.

HABITAT A very sparsely and intermittently distributed duiker ranging from the R. Sanaga to Rwenzori and the West Rift, but only north of the Congo R. It does not occur in extensively flooded forests and is known to be common in only a few highly localised places (notably N Gabon and Congo).

FOOD A ratio of 73% fruits to 25% foliage (and a marked taste for flowers) has been recorded in Gabon. Hard-shelled fruits (among them Mututu, *Klainedoxa*) in the diet implies that this duiker might smash them open (probably with the forehead).

STATUS A sample of hunters' bags in DR Congo showed this species to be the least frequently caught duiker (thought to be a measure of low density and elusiveness). It is found in several reserves but is likely to be one of the earliest animals eliminated as the commercial bushmeat trade gathers momentum. Widespread but locally vulnerable. Currently not endangered overall.





Natal Red Duiker

NATAL RED DUIKER *Cephalophus natalensis*

OTHER NAMES Fr. *Céphalophe du Natal*. Ger. *Rotducker*. Swah. *Funo, Ngarombwi*.

MEASUREMENTS HB 750–870mm. T 90–140mm. Sh. ht 400–430mm. W 12–14kg.

RECOGNITION A small duiker with red body, legs and frontal tuft. The neck may be red or pale grey. Margins of the ears, chin, throat and underside of the tail are white. The upperside of the tail, ears and muzzle are black.

GEOGRAPHIC VARIATION Four subspecies have been named, some of which may be invalid. Southern populations tend to be red overall (*C. n. natalensis*). Northern populations often have grey on the upper neck (*C. n. robertsi*).

HABITAT From central Natal to the R. Rufiji valley, inhabiting coastal forests and thickets, low-lying riverine growth, escarpment and montane forests east of L. Malawi (L. Nyasa) and the R. Shire. A diversity of trees that may flower and fruit through most of the year are prerequisites for its presence.

FOOD Opportunistic; fruits, flowers and foliage. All feeding is normally diurnal but the animal may become nocturnal in very disturbed areas.

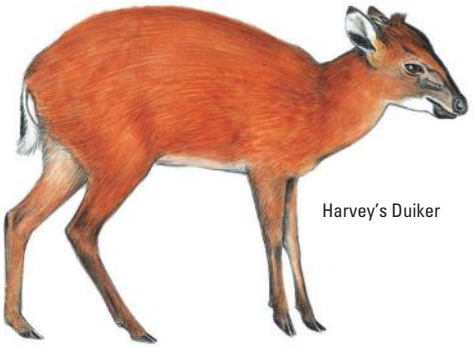
STATUS The Natal Red Duiker is still widespread and common, but rarely seen, in spite of intensive hunting and trapping over most of its range. Conversion of its habitat for settlement and agriculture is proceeding rapidly in many parts of its extensive but already fragmented range. Not yet endangered.

HARVEY'S DUIKER *Cephalophus harveyi*

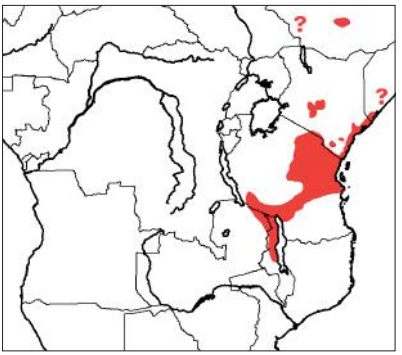
OTHER NAMES Fr. *Céphalophe de Harvey*. Ger. *Harveyducker*. Swah. *Funo*.

MEASUREMENTS HB 850–950mm. T 110–150mm. Sh. ht 440–500mm. W 13–16kg.

RECOGNITION A rich red duiker with a black line down the centre of the face and nape. In most parts of its range it has dark legs and a black-and-white chin. The white-lined, tufted ears are black-tipped.



Harvey's Duiker



Harvey's Duiker

GEOGRAPHIC VARIATION This species appears to hybridise with *C. natalensis* in the region of Dar es Salaam and with *C. weynsi* in the Mau, central Kenya. *C. h. bottegoi* has been named from the coast in the Somali–Kenya border area.

HABITAT From coastal thickets to montane forests, riverine gallery and secondary forests wherever there is a variety of fruiting and flowering trees and shrubs. It ranges from the south Somali coast to the mainland opposite Zanzibar I. and across the mountains of E Kenya and Tanzania to Malawi and Nyika Mt.

FOOD Fruits, flowers and foliage from the forest floor. Diurnal.

STATUS Widespread and common but declining as its habitats become degraded or destroyed for charcoal or agricultural land.

RED-FLANKED DUIKER *Cephalophus rufilatus*

OTHER NAMES Fr. *Céphalophe à flancs roux*. Ger. *Rotflanken ducker*.

MEASUREMENTS HB 600–800mm. T 70–100mm. H 300–38mm. W 6–14kg.

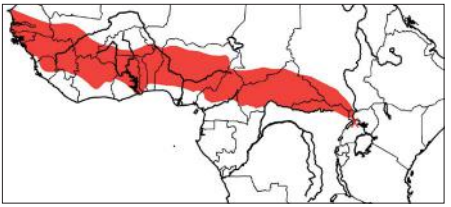
RECOGNITION Prettily coloured with bright orange-red on the face, neck and flanks, brown or blue-grey gauntlets on the limbs and a brown or grey dorsal patch which has pale grey underfur. The black nose and lower lip contrast strongly with white jaws and upper lip. The ears have black and white flashes. The nose is straight and the skull narrow. Relative to its size it has the largest preorbital glands of any duiker. This indicates exceptionally active marking behaviour.

GEOGRAPHIC VARIATION *C. r. rufilatus* (Senegal to the Chari and Benue valleys), *C. r. rubidior* (Chari to Nile valleys).

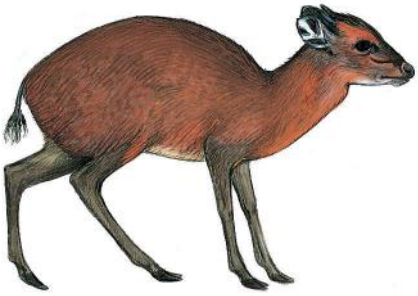
HABITAT A resident, territorial species living in forest relicts and riverine thickets within the savanna along a broad band of country from Senegal to NW Uganda.

FOOD Fruits, flowers and foliage from numerous riverine species of trees, shrubs and herbs.

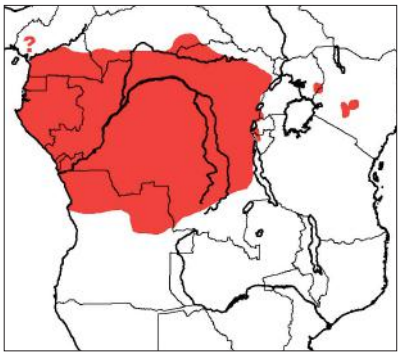
STATUS This species can withstand considerable hunting pressure as long as enough suitable habitat remains available. It is in decline in very heavily settled areas but is still widely distributed. Listed as not endangered (IUCN).



Red-flanked Duiker



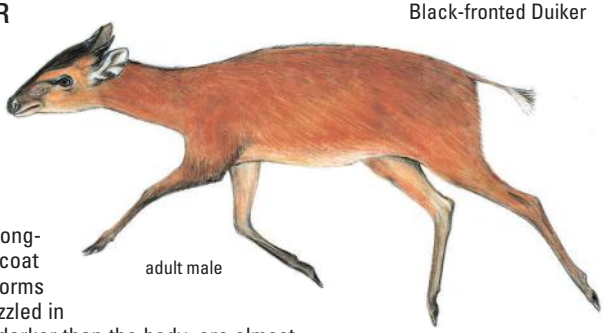
Mt Kenya Black-fronted Duiker *C. n. hooki*



Black-fronted Duiker

BLACK-FRONTED DUIKER

Cephalophus nigrifrons



adult male

OTHER NAMES Fr. *Céphalophe à front noir*. Ger. *Schwarzstirnducker*.
MEASUREMENTS HB 800–1,070mm. T 75–150mm. Sh. ht 450–580mm. W 14–18kg.
RECOGNITION A long-legged, long-hoofed duiker with glossy red coat that is plain and thin in lowland forms and thicker, darker and more grizzled in montane forest forms. The legs, darker than the body, are almost black at the hocks and thinly haired. There is a distinct pale 'brow' below the black forehead blaze that gives it its name.
GEOGRAPHIC VARIATION *C. n. nigrifrons* (lowland forest from Cameroon to E DR Congo), *C. n. kivuensis* (W Rift mountains and volcanoes), *C. n. fosteri* (Mt Elgon), *C. n. hooki* (Mt Kenya).
HABITAT From Cameroon to Mt Kenya, where they are adapted to swamp forest and marshes at both low and high altitudes (up to 3,500m.). Like other duikers, they have territories marked out with face glands and a loud whistling call. They also make a loud thumping sound in the chest (the vocal equivalent of a typical bovid foot-stamp?). They follow regular paths from night shelters to day-time feeding grounds in swamp.
FOOD A variety of fruits and succulent vegetation, including balsam (*Impatiens*), Wild Coffee and other Rubiaceae. A ratio of 72% fruits to 28% foliage has been recorded in a fruit-rich Gabonese forest.
STATUS Widely distributed but in Kenya appears to have been hunted-out in the Aberdare Mts, and also vulnerable to intensive hunting on Mt Elgon.

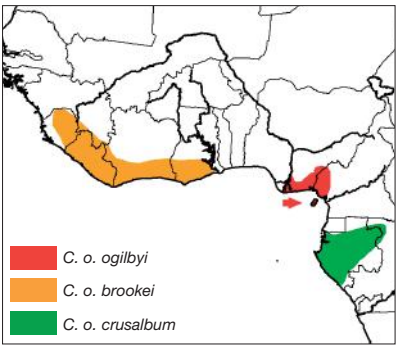
OGILBY'S DUIKER *Cephalophus ogilbyi*

OTHER NAMES Fr. *Céphalophe d'Ogilby*. Ger. *Ogilbyducker*.
MEASUREMENTS HB 850–1,150mm. T 120–150mm. Sh. ht 550–560mm. W 14–20kg.
RECOGNITION Orange to mahogany-coloured duiker with a very red rump, a paler underside, and a black dorsal line (of variable extent). The face has marked brows and short but peculiarly curved horns with strong corrugations (in both sexes). Legs vary in colour. The tail is short and tufted. This species has massive hindquarters, a deep, slab-sided body and long, slender legs.
GEOGRAPHIC VARIATION Ogilby's Duiker *C. o. ogilby* (Bioko I. and Cameroon/Nigeria borderlands), Brooke's Duiker *C. o. brookei* (Sierra Leone to Ghana), White-legged Duiker *C. o. crusalbum* (Gabon). These forms might merit species status.
HABITAT Primarily forests close to the West African coast, where it is now rare and patchily distributed. On Bioko I., it was a common and dominant species, notably on the less disturbed upper slopes of the mountains. The absence of other large duikers is clearly a factor in this.

Ogilby's Duiker *C. o. ogilbyi*

White-legged Duiker *C. o. crusalbum*

Brooke's Duiker *C. o. brookei*



Ogilby's Duiker

FOOD Mainly fallen fruits, with the large, hard fruits of mututu (*Klainedoxa*) noted. The distribution of this species might be influenced by a super-abundance of fibrous fruits and numerous primates that contribute to the fruit-fall.

STATUS Habitat destruction and degradation threatens *C. o. brookei* with extinction everywhere, except in the Korup NP. *C. o. crusalbum* will only be secure if logging is stopped in the Lopé Reserve. *C. o. ogilby* is not currently endangered but requires the implementation of national park status for the Caldera de Luba on Bioko I. and control of the burgeoning urban bushmeat trade.

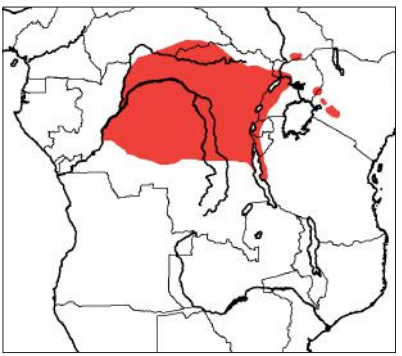
WEYNS'S DUIKER *Cephalophus weynsi*

OTHER NAMES Fr. *Céphalophe de Weyns*.
Ger. *Weynsducker*.

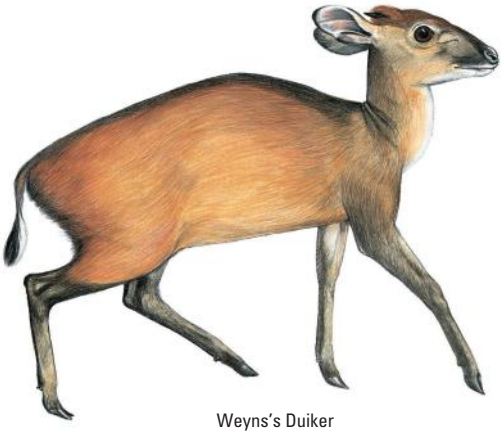
MEASUREMENTS HB 800–1,150mm. T 80–160mm. Sh. ht 450–600mm. W 15.5–20kg.

RECOGNITION A fairly large duiker of very variable colouring. The main body colouring can range from pale tawny to rich russet or dark brown. The dark brown may be confined only to the legs or tint the shoulders, neck and face. The frontal tuft is russet in all subspecies. The forehead is among the most heavily reinforced of any duiker, with the dense bone of the frontal up to 13mm thick in some males.

GEOGRAPHIC VARIATION *C. c. weynsi* (R. Ubangi to Victoria Nile), *C. c. barbertoni* (E Uganda, W



Weyns's Duiker



Weyns's Duiker

Kenya), *C. c. lestradei* (north end of L. Tanganyika). (Supposed hybrids with *C. harveyi* on Mau, Kenya.)

HABITAT Ranges from R. Ubangi to W Kenya in both lowland and montane areas. This diurnal and territorial species flourishes in regenerating patches after logging but is not found in outlying riverine strips and galleries.

FOOD About 70% of the diet consists of both ripe and unripe fruits. Fallen foliage made up most of the balance.

STATUS A preferred prey of forest hunters but, in the absence of serious forest degradation, it seems able to withstand light but regular hunting. It is now rare or vulnerable in Burundi, Rwanda, Kenya and Uganda.

PETERS'S DUIKER *Cephalophus callipygus*

OTHER NAMES Fr. *Céphalophe de Peters*. Ger. *Petersducker*.

MEASUREMENTS HB 940–1,090mm. T 80–150mm. Sh. ht 450–600mm. W 17.5–25.2kg.

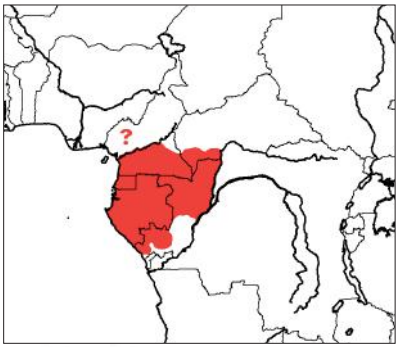
RECOGNITION A fairly large duiker with a rich-red rump graduating into tawny flanks, neck and cheeks. Bright russet frontal tuft. A black mid-dorsal stripe widens over the hindquarters. The belly has a sepia midline that broadens on the chest. White flashes on ears, chin and lips. Like *C. weynsi*, the forehead is reinforced with a dense bony frontal.

GEOGRAPHIC VARIATION None, but individuals have been photographed that appear to have hybridised with *C. ogilbyi*. If so, it is possible that *callipygus* is actively replacing and interbreeding with *C. ogilbyi*.

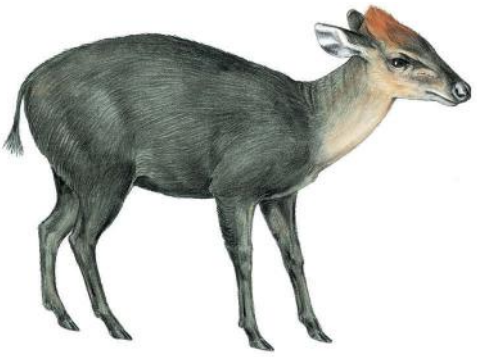
HABITAT Ranges through the moist equatorial forest zone from the R. Sanaga in Cameroon to the R. Ubangui. A diurnal and territorial species that even occurs in regenerating patches after logging so long as fruit and monkeys remain, but not in outlying mosaics or galleries. It occasionally survives in farm-bush.

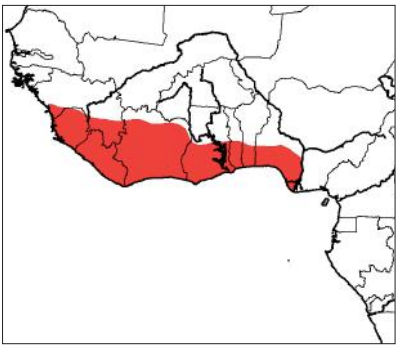
FOOD Recorded as taking 83% fruits and only 16% leaves (at Makoku, Gabon). This was the most completely frugivorous of all the duikers studied there.

STATUS Can withstand regular hunting and is known to exist at densities of up to 20 per km^2 in Gabon. As a preferred species for commercial bushmeat trade, offtake levels are unsustainable in more settled areas.



Peters's Duiker





Black Duiker

BLACK DUIKER *Cephalophus niger*

OTHER NAMES Fr. *Céphalophe noir*. Ger. *Schwarzducker*.
MEASUREMENTS HB 800–1,000mm. T 70–140mm. Sh. ht 450–550mm. W 16–24kg.
RECOGNITION A heavily built, long-bodied, long-headed, glossy black duiker with swollen nostrils and short, stocky legs. The coat pales to light grey around the throat and chin and the lining of the ears. The tail shows some white hairs. Short horns, normally present in both sexes, are largely hidden in a coronal tuft of dense reddish hair.
HABITAT Rainforest from Sierra Leone to SW Nigeria, also survives in some riverine galleries, isolated patches and semi-deciduous forests on the margins of its range. It can also survive in regeneration areas after logging. It is mainly diurnal and territorial and is thought to fill a similar niche in Upper Guinea to Peters's Duiker, *C. callipygus*, in central Africa.
FOOD Fallen fruits and flowers, leaves and herbs. The Black Duiker is presumed to be as dependent on year-round fruit fall as other largish duikers.
STATUS This species suffers from overhunting throughout its range, except in some remote or better-protected localities in Liberia, Ivory Coast and Ghana. It is rare and endangered in Sierra Leone, Togo and Nigeria. Still widespread, its supposedly 'satisfactory' IUCN status will change unless curbs are put on the ever more voracious and cruel bushmeat trade.

ABBOTT'S DUIKER *Cephalophus spadix*

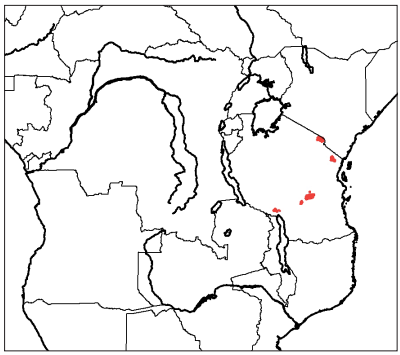
OTHER NAMES Fr. *Cephalophe d'Abbott*. Ger. *Abbottducker*. Swah. *Minde*.
MEASUREMENTS HB 970–1,400mm. T 80–130mm. Sh. ht 660–740mm. W 50–60kg.
RECOGNITION A large, glossy, nearly black duiker with a paler grey face, a very prominent russet tuft between the horns and a reddish tinge to the belly and lower flanks. The wedge-shaped head ends with a broad, flat-fronted nostril pad that overhangs the mouth (as with Yellow-backed Duikers). Overall, this is a stocky duiker with rather short, thick legs and a thick neck.

HABITAT Montane forest duiker restricted to the wetter (and therefore mainly eastern) sides of a few isolated massifs in E and S Tanzania. It is commonest in the Kilimanjaro NP and Forest Reserve between 1,300 and 2,700m in forest and high-altitude swamps, but is said to range up to 4,000m and has been seen in high-altitude scrub and moorland. It formerly

occurred above L. Manyara, in the Uluguru and Usambara Mts. It just survives on Mt Rungwe and in the Uzungwa mountain range. Disturbance may drive this species into more nocturnal activity but its preference for dense cover and its alertness keep it from view.

FOOD Fruits, flowers, green shoots and herbage; recorded browsing Balsam (*Impatiens*).

STATUS Although Abbot's Duiker is protected by law and occurs in the Kilimanjaro NP, this species is acutely threatened by poaching and the destruction of its habitat for charcoal, logs and potato fields. The Udzungwa and proposed Chita National Parks will be essential for the long-term survival of this forest endemic.



Abbott's Duiker

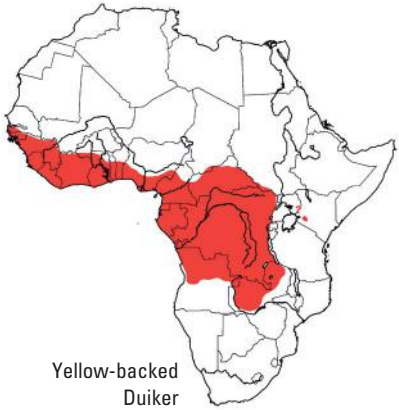
YELLOW-BACKED DUIKER

Cephalophus silvicultor

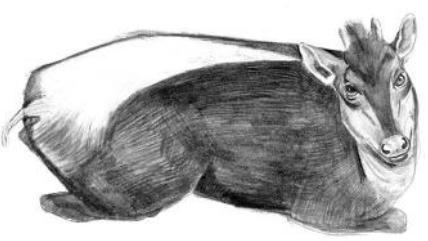
OTHER NAMES Fr. *Céphalophe à dos jaune.* Ger. *Riesenducker.* Swah. *Kipoke.*

MEASUREMENTS HB 1.25–1.90m. T 110–200mm. Sh. ht 650–870mm. W 45–80kg.

RECOGNITION A large, greyish-brown duiker with a vivid cream-coloured patch on the back. The long, wedge-shaped head has a light grey muzzle and cheeks ending in a shiny black rhinarium. Eyes and ears are small. The horns can be as long as 210mm. Newborn calves are dark umber, with freckled sides and a deep reddish tinge all over the underparts. The centre of the back is all jet black and only changes to adult colouring by 9 months of age. Juveniles at intermediate stages of growth can be difficult to identify.



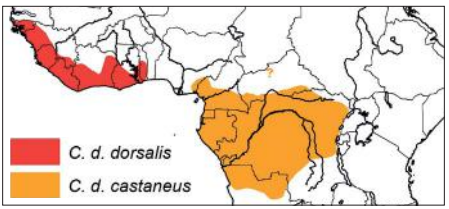
Yellow-backed Duiker



Yellow-backed Duiker

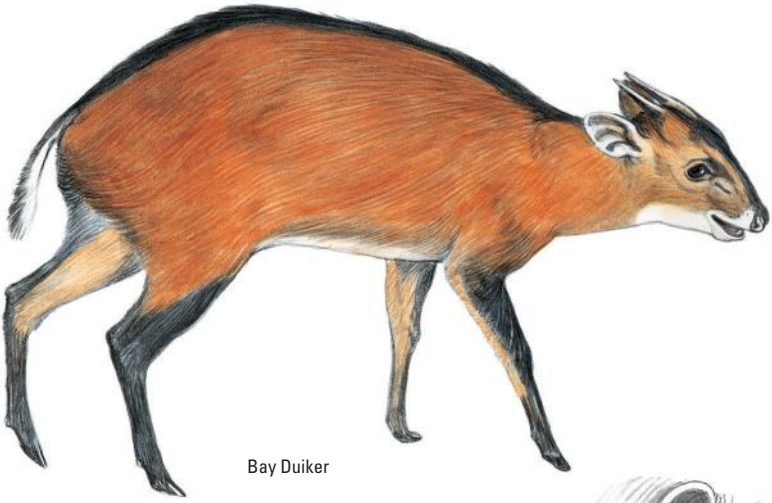
GEOGRAPHIC VARIATION Nine subspecies are described but some are likely to be within the normal range of variation. Four subspecies are provisionally recognised here: *C. s. silvicultor* (Senegal to Niger delta), *C. s. longiceps* (Niger delta to Nile headwaters), *C. s. curticeps* (mainly eastern and central African montane form), *C. s. ruficrista* (south of Congo R. basin).
DISTRIBUTION Senegal to SW Sudan and discontinuously to W Kenya. Angolan littoral to western shores of L. Tanganyika.
HABITAT Rainforest, montane forests and many permutations of forest-savanna mosaics, from narrow riverine strips to fragmented woods. It is often found close to deep swamps. It lies up singly in characteristic 'forms' at the base of large trees, under fallen trunks or in dense tangles. It likes to shelter from rain (and may even use the remnants of a pit-sawer's or hunter's lean-to). As many as six such resting places can be found within 1km^2. Throughout its range it lives only in pockets of suitable habitat where it can be quite numerous. It is attracted to salt-licks.
FOOD Fallen seeds, fruits, berries and the bark of shrubs, fungi, ground moss and many herbs. In montane areas, Waterberry (*Syzygium*), Dog Plum (*Ekebergia*) and Yellowwood (*Podocarpus*) are favoured fruits. In lowland forests Stem-fruit (*Chrysophyllum*), African Mangosteen (*Garcinia*) and Duiker Tree (*Sapium integerrimum*) have been recorded. Kudu Berry (*Pseudolachnostylis maprouneifolia*), raisin trees (*Canthium*), and snake beans (*Swartzia*) are savanna or forest-edge plants taken in the south of its range.
BEHAVIOUR This duiker is mainly solitary and spaced out in territories (probably shared by a male and female). Lying up on 'observation posts' on termite mounds suggests that surroundings are regularly monitored and broken male horns could indicate active defence of territory by males.
One, rarely two, young are born after a 151-day gestation. The newborn lies tight for a week or more but starts to nibble vegetation almost at once. It grows rapidly and is weaned by 6 weeks. The horn buds appear after about a month, when light hairs begin to show in the black back. Animals reach adult proportions and colouring by 9 months and are sexually mature by 1 year. Adults communicate with resonant grunts and a shrill bleat.
ADAPTATIONS The yellow back is not as conspicuous in the field as one might suppose because the hair lies close, reducing the pale colour to no more than a streak. The hair can be erected in display but this has only been observed in captivity in response to disturbance. It is probable that the yellow back has a social function. It may cover glandular skin, but this has yet to be verified.
STATUS Widespread and common in many parts of its range, recent reports from Kenya suggest that it may have become endangered there, as it has in Gambia. Over much of the rest of its range it is declining but not yet endangered.

BAY DUIKER *Cephalophus dorsalis*



Bay Duiker

OTHER NAMES Fr. *Céphalophe bai*.
Ger. *Schwarzruckenducker*.
MEASUREMENTS HB 700–1,000mm. T 80–150mm. Sh. ht 400–560mm. W 15.0–24.5kg.
RECOGNITION Heavily built duiker with a red or yellowish-brown coat, black or dark-brown legs and a black midline along back and belly (definition varies individually). The fur is coarsely textured. The muzzle is extremely reduced and strongly tapered. The eyes are larger and higher in the head and the entire head is broader and flatter than in any other duiker, due to its enlarged cheek muscles (for lateral chewing action).
GEOGRAPHIC VARIATION *C. d. dorsalis* (Senegal to Togo), *C. d. castaneus* (E Nigeria to E DR Congo).
HABITAT The entire equatorial lowland rainforest block from Senegal to L. Tanganyika, with a preference for high primary rainforest. Also patches within savanna mosaics (if undisturbed).



Bay Duiker

Head of Bay Duiker female indicating vibrissae embedded in white 'signal' patches above eye and behind rhinarium.

Within the rainforest zone they may visit edges of clearings and prefer well-diversified zones with both dry and waterlogged areas. They shelter in hollow trees, between butresses, under fallen trunks and in dark, dense thickets, only emerging to feed at night. They live at a lower density than other duikers and even in the richest habitats it has been estimated that two or three animals inhabit 12–20ha.

FOOD Hard or fibrous fruits, such as wild mango (*Irvingia*), mututu apples (*Klainedoxa*), African Breadfruit (*Treculia africana*), and white star apple (*Chrysophyllum*), have been recorded; also less difficult fruits, such as monkey orange (*Strychnos*) and yellow mulberry (*Myrianthus*). Bay Duikers are also known to stalk, kill and eat birds but fruits accounted for 73%, and foliage 27%, in a Gabon sample.

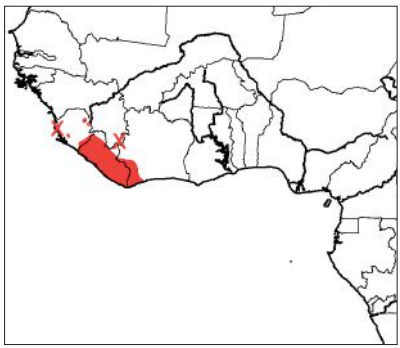
STATUS A very widespread species but a popular quarry for hunters. Declining in many West African countries, this species is now rare in Nigeria and Sierra Leone and extinct in Uganda. Overall not yet endangered.

JENTINK'S DUIKER *Cephalophus jentinki*

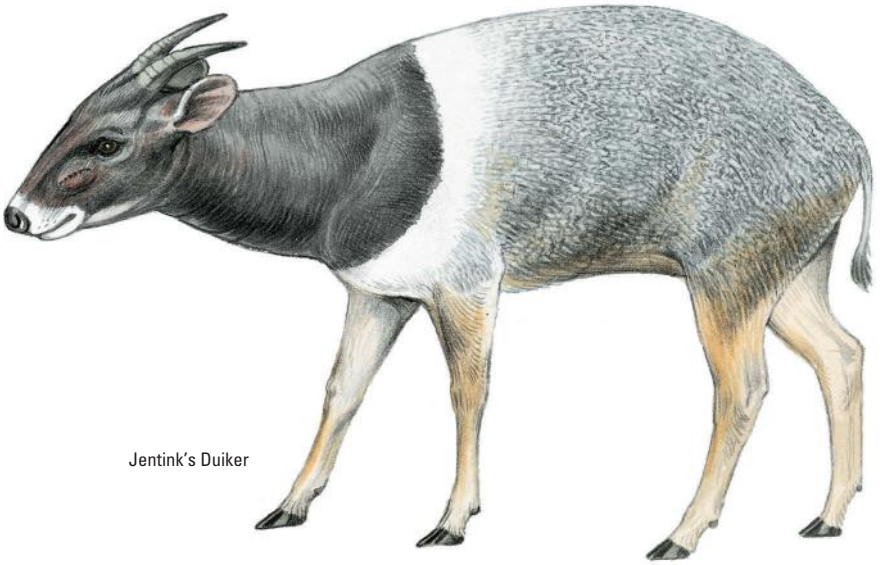
OTHER NAMES Fr. *Céphalophe de Jentink*. Ger. *Jentinkducker*.

MEASUREMENTS HB (est.) 1.3–1.5m. T (est.) 120–160mm. Sh. ht (est.) 0.75–1.0m. W (est.) 50–80kg.

RECOGNITION A long-horned (up to 170mm), very robust, short-legged duiker with a bold pattern of black, white and grey (its early name of 'forest goat' was not entirely inappropriate). The nearly black head and neck are offset by a vivid white halter over the shoulders and lower chest and a white border surrounds the mouth and nose. This presents a symmetrical oval when viewed from in front. The colouring involves both skin and fur, the latter being



Jentink's Duiker



Jentink's Duiker

extremely short and fine. In contrast to the fore-end the hindquarters are grey agouti (this grizzled fur giving it a local name of 'squirrel-duiker').

HABITAT Only found in the high primary forest zone between Sierra Leone and the R. Niouniourou, a distribution that broadly coincides with many monkey populations and also that of the Zebra Duiker (see map, p.535). Within this zone, it enters secondary growth, scrub, farms, plantations and is even known to visit the seashore, presumably for salt. It is a 'hider', choosing hollow trees, fallen trunks and the buttress bays of Kapok (*Ceiba*), *Bombax* and Mututu Trees (*Klainedoxa*) for shelter. Unusually for duikers, it sometimes lies up in pairs. Like the Bay Duiker, it bolts from these day-time refuges with great speed if discovered, but has no stamina and does not go far. It is very residential and supposedly territorial but makes nocturnal forays out of thick forest, especially during periods when fruit is scarce. It is so secretive that it continued to survive less than 30km from Freetown, a city of half a million people, hiding on steep, densely forested slopes in the city's water catchment area. Its most basic requirements appear to be a diversity of fruiting trees and very dense shelter rather than a specific forest type.

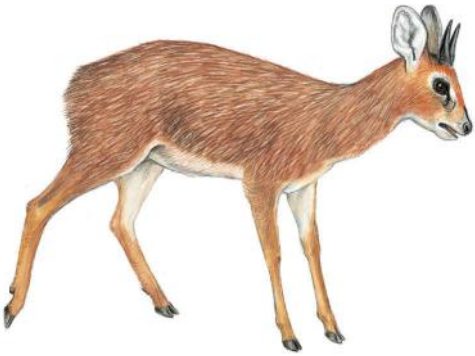
FOOD Known to enter plantations to eat palm nuts, mangoes and cocoa pods. The growing stems of tree seedlings are eaten (African Teak, *Chlorophora excelsa*, has been identified). Hunters familiar with the duiker's habits have identified many fruits with hard seeds or shells, notably kola nuts, erimado (*Ricinodendron*), Cherry Mahogany (*Tieghemella heckelii*), sand apples (*Parinari*) and Tallow Tree (*Pentadesma butyracea*). Jentink's Duiker has also been reported chewing roots after exposing them with its hooves.

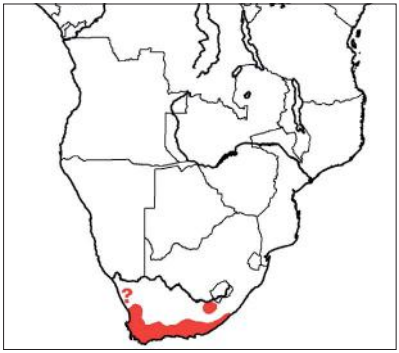
STATUS Reportedly common in Sierra Leone at the turn of the century (before commercial loggers stripped the forests), it is now found only in the few remaining areas of undisturbed forest where hunting is now intensifying. Likewise, in Liberia, a new generation of commercial bushmeat hunters is now entering formerly remote areas to take out meat (mostly smoked in situ). This form of asset-stripping is nominally prohibited in Sierra Leone and Côte d'Ivoire but is legal in Liberia, the centre of the duiker's range, and still its main stronghold. Listed as endangered (IUCN) in Sierra Leone and Côte d'Ivoire. It is endangered by new hunting and snaring practices in Liberia.

GRYSBOKS Raphicerini

Cape Grysbok	*Raphicerus melanotis*
Sharpe's Grysbok	*Raphicerus sharpei*
Steenbok	*Raphicerus campestris*
Beira	*Dorcatragus megalotis*

Of all living antelopes, the Cape Grysbok, *Raphicerus melanotis*, provides the closest approximation to an ancestral type. It also resembles the earliest currently known antelope fossil, the 16-million-year-old *Eotragus* (from Eurasia).





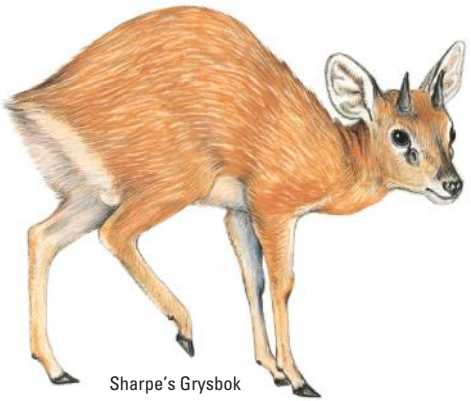
Cape Grysbok

CAPE GRYSBOK *Raphicerus melanotis*

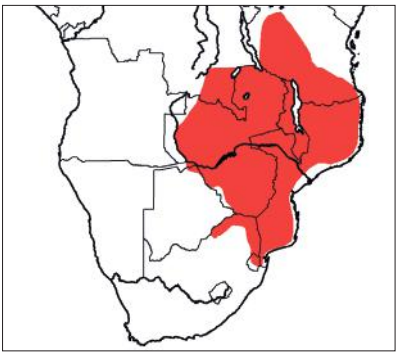
OTHER NAMES Fr. *Grysbok du Cap*. Ger. *Kaapgreisbock*.
MEASUREMENTS HB 650–800mm. T 40–80mm. Sh. ht 450–550mm. W 8–12kg. (♀ 0.5kg heavier).
RECOGNITION A thick-coated, chunky little antelope with russet-brown fur densely interspersed with white hairs to give a 'strawberry roan' colour to the body. There is less white flecking on the head, neck and legs, which are yellower in tint. The ears are very large and lined with white hair. The short, blunt muzzle has a black bridge to the nose and a shiny black nostril pad and lips. Males have short, sharp and smooth horns (normally about 80mm long) which are widely spaced. Rump fur can be fluffed out to increase the impression of size. The tail is short and inconspicuous.
HABITAT A Cape relict species found between Albany and the Cedarberg Mts. It lives in scrub-covered sand dunes and thickets bordering rocky hills and steep gorges but also shelters in reedbeds or along riverbeds along the southern margins of the Karoo. It is probably territorial and is usually seen singly. The young, born after a 6-month gestation, are hiders and grow fast. Most young are born between September and December (summer).
FOOD Browser of thicket and shrubby growth. Although the Cape Grysbok is active during the morning and late afternoon during winter, it is mainly nocturnal (possibly influenced by disturbance).
STATUS As the closest approximation to the model of an antelope ancestor, the survival and study of this species is of great importance. In spite of greatly retracted habitats it is still common within its localised range and in numerous parks and reserves. Listed as not endangered (IUCN).

SHARPE'S GRYSBOK *Raphicerus sharpei*

OTHER NAMES Fr. *Grysbok de Sharpe*. Ger. *Sharpegreisbock*.
MEASUREMENTS HB 610–750mm. T 50–70mm. H 450–600mm. W 7.0–11.5kg.
RECOGNITION A small antelope with a 'skirt' of elongated fur over the hindquarters. The reddish-fawn fur is densely interspersed with white hairs. The face, throat and underside are much paler, even off-white. Horns (present in males only) and eyes are widely spaced and the muzzle is short but deep, with a large mouth and robust cheek teeth. The moderately large ears are mounted on a



Sharpe's Grysbok



Sharpe's Grysbok

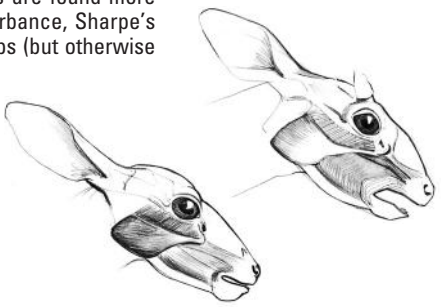
thick base (resembling the Klipspringer in this respect). Its 'tipped-up' rump posture while grazing herbs results from a short neck and face on a relatively long-legged body.

GEOGRAPHIC VARIATION Two subspecies have been named but are probably invalid.

HABITAT Ranging from L. Victoria to the Transvaal, the Zambezi watershed approximates to its western limits. Within this extensive area it is generally scarce and localised, preferring low thicket and secondary growth, stony outcrops and broken uplands, where it favours fertile zones on the lower foothills. It is predominantly nocturnal and lives in territories where pairs may form a loose association but are usually seen singly. Middens are found more easily than the animals themselves. At any disturbance, Sharpe's Grysbok departs rapidly, with short, stamping hops (but otherwise silently). It has been reported hiding in Aardvark burrows. In southern Africa a birth peak during the summer rains has been suggested.

FOOD Browses leaves, buds, herbs and fruits in a habitat where dry-season vegetation is generally tough. The teeth and jaw are well suited to such a diet and *Acacia*, raisin bush (*Grewia*), buffalo thorn (*Ziziphus*), ebony (*Diospyros*), and various fruits and berries have been recorded, along with grass (about 30%).

STATUS Probably declining generally but impossible to assess accurately because of its extreme shyness. Not endangered overall but locally rare.



Facial myology of *Raphicerus* spp. compared, showing mouths predominantly adapted to browsing, Sharpe's Grysbok *R. sharpei* (*above*) and to grazing, Steenbok *R. campestris* (*below*).

STEENBOK *Raphicerus campestris*

OTHER NAMES Steinbok, Steinbuck. Fr. *Steenbok*. Ger. *Steinbockchen*. Swah. *Isha, Dondor*.

MEASUREMENTS HB 700–950mm. T 40–60mm. H 450–600mm. W 7–16kg.

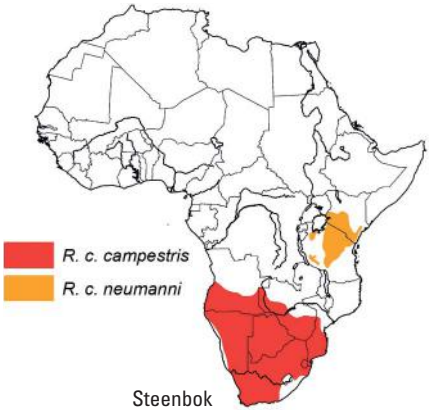
RECOGNITION More slender than a Bush Duiker, less so than an Oribi, the Steenbok can be mistaken for either but has characteristically rounded haunches without visible tail, very large, white-lined ears, a retroussé, black-bridged nose and big, black-rimmed eyes encircled by white. The males have very upright, polished spike horns. Colour ranges from pale brown to fawn or bright rufous.

GEOGRAPHIC VARIATION *R. c. campestris* (southern Africa, 24 listed), *R. c. neumanni* (East Africa).

DISTRIBUTION All of southern Africa from Angola to near the mouth of the R. Zambezi. East Africa on both the Kenya coast and open plateaus and savannas inland up to 4,750m. Scarce or absent in most Miombo (*Brachystegia*) woodland areas.

HABITAT In southern Africa they are mainly open-plains animals. In East Africa they are common in stony savannas and among Acacia–grassland mosaics. Steenbok favour transitional and unstable conditions, following bush-clearance by cultivation, roads or elephants, often under a very dry

Steenbok



Steenbok

climate. In open plains they tend to focus on riverbeds or belts of thicket where they can find well-hidden, regularly used resting places or refuges.

FOOD Browsers at or near ground level and adept at scraping up selected roots and tubers with hard, sharp hooves. Steenbok favour shoots of dominant shrub and tree species, such as *Acacia*, Leadwood (*Combretum imberbe*), buffalo thorn (*Ziziphus*), *Bridelia* and Mopane (*Colophospermum mopane*). They also take fruits and, during periods of early growth, may graze almost wholly on sprouting grass. They can survive without water and may live as far as 80km from water in the Kalahari subdesert.

BEHAVIOUR Pairs are thought to live for long periods with the same partner on the same territory (4ha to 1km^2). Members of such pairs appear to move and rest independently but observers have suggested that routines and scent cues could keep such pairs mutually aware of one another's movements and position much of the time. In the absence of territory-marking with face glands (which are very small in Steenbok) the principal scent beacons are dung middens. These are connected by trails laid by secretions that ooze from glands between the hooves. Middens are scraped following defecation (by both sexes). It is possible that this associates individual 'signatures' in dung and urine with less specific hoof scents. The reception of such subtle clues is enhanced by the fact that most of the Steenbok's foraging is on or just above the soil surface.

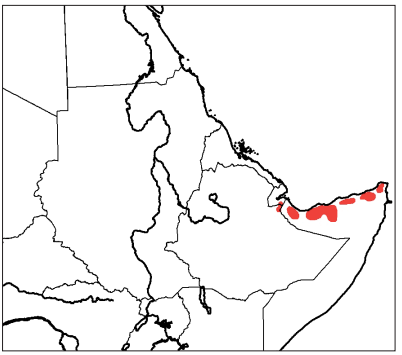
A territorial male becomes very aggressive during his female's oestrus. Following a gestation of about 170 days a precocious fawn is born which remains well hidden for 2 weeks (in spite of being able to walk in 5 minutes) before joining its mother foraging. Lactation lasts 3 months and by 6–8 months female offspring are fertile. Some males are thought to breed twice a year, and this fecundity may explain their persistence in parts of South Africa in spite of sustained persecution. Animals live for at least 7 years.

Steenbok, male

ADAPTATIONS As a first line of defence Steenbok resort to the infantile strategy of sinking to the ground and freezing, ears retracted, while attentively watching any approaching danger. Their second strategy is to flee if the danger draws too close. Fast, zigzag flight alternates with repeated attempts at prostrate concealment. Both are compromise defences in a small conservative antelope that has invaded environments very different from those to which other *Raphicerus* are adapted.

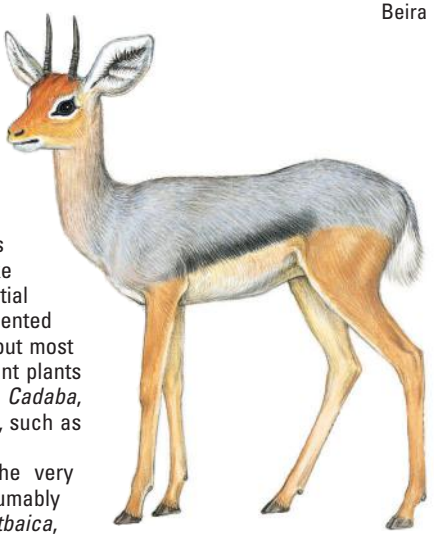
STATUS Although this species has been exterminated from many small localities, it is still common in suitable habitats. Overall status, not endangered.

BEIRA *Dorcatragus megalotis*



Beira

OTHER NAMES Fr. *Beira*. Ger. *Beira*.
MEASUREMENTS HB 760–870mm. T 50–80mm. H 500–760mm. W 9–12kg.
RECOGNITION A very long-legged, long-necked antelope with enormous ears, vertical, upright horns (90–130mm) in the male only, and goat-like hooves which have rubbery centres and are especially rounded on the hindlegs. The coarse, thick fur is grey on the back and neck, graduating into a broad, oblique stripe of very dark grey from elbow to thigh. The underparts, throat and inner limbs are cream while the outer limbs and cheeks are ochre yellow. The forehead and nose (with hairy, slit nostrils) are covered in short, bright russet fur. The lids of the eyes are intensely black, contrasting strongly with their surround of brilliant white fur. The ears are also made conspicuous by dense white hair tracts.
DISTRIBUTION Confined to hills and mountains in N Somalia, notably the Migiurtina, Warsengeli Xadeed, Buuraha and Marmar ranges where it favours loose rubble screes.
HABITAT Usually close to stony ridges, gorges and plateau margins (where the Beira can make a quick get-away and break contact with potential predators). The extensive fields of finely fragmented stone in which it lives support scattered bushes but most plant growth is dwarfed or stunted. Some dominant plants in the preferred habitat are *Acokanthera*, *Buxus*, *Cadaba*, *Cadia*, *Carissa*, *Dodonaea* and various succulents, such as aloes, euphorbias and *Sansevieria*.
FOOD Beira have been observed feeding on the very common shrimp plant, *Justicia*. The Beira presumably browses the scattered shrubs, notably *Acacia etbaica*, while there is fresh growth on them but relies for its staple food on very small herbs growing among the pebbles. *Solanum*, *Cordia* and *Hibiscus* species have all been recorded.



BEHAVIOUR Usually seen in pairs or parties with a single male. Larger groups, up to 12, are possibly temporary associations of two neighbouring families. Such aggregations are rarely seen and may include two adult males. Each group is intensely attached to its own hillside or plateau. Gestation is estimated to last about 6 months and births have only been recorded in April (the peak of the rains).
ADAPTATIONS Exposure to predators in an open environment demands speed. Stamina is less critical where any pursuer is less well adapted to the terrain than the pursued. Extensive home-ranges and a scarcity of prominent landmarks help to explain the Beira's suppression of scent glands and overt marking behaviour. However, its ground-level foraging might have favoured the retention of pedal glands between the hooves. The raised rubbery cushions behind the hoof's margins are specifically adapted to walking and running on its very difficult terrain. The Beira's huge ears allow it to hear any approach across the loose stones, a capacity confirmed by its celebrated wariness and its survival in a region where many other species have become extinct.
STATUS The Beira's limited range, the absence of any protected areas within it, uncontrolled hunting, habitat degradation and competition from goats must all prejudice its long-term survival. It was thought to have made a slow recovery after dying in large numbers during the very severe 1975 drought. Nonetheless, its extreme specialisation for a very difficult and marginal habitat should continue to favour its survival for some time. The only viable captive breeding group is currently held in a private collection at Al Wabra (Qatar). Listed as threatened with extinction (IUCN).

DIKDIKS Madoquini

Formerly included within the Neotragini (when that taxon embraced all the dwarfed antelopes). Contemporary genetic research has demanded the disaggregation of Neotragini and the recognition that the dikdiks represent a lineage that has been distinct for more than 10 million years.

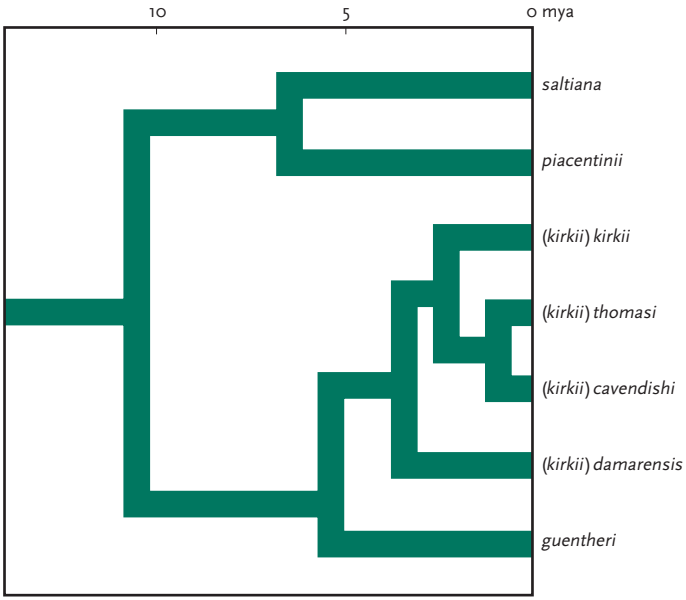
DIKDIKS *Madoqua*

Salt's Dikdik	*Madoqua saltiana*
Silver Dikdik	*Madoqua piacentinii*
Kirk's Dikdik species group	*Madoqua (kirkii)* (4 species)
Günther's Dikdik	*Madoqua guentheri*

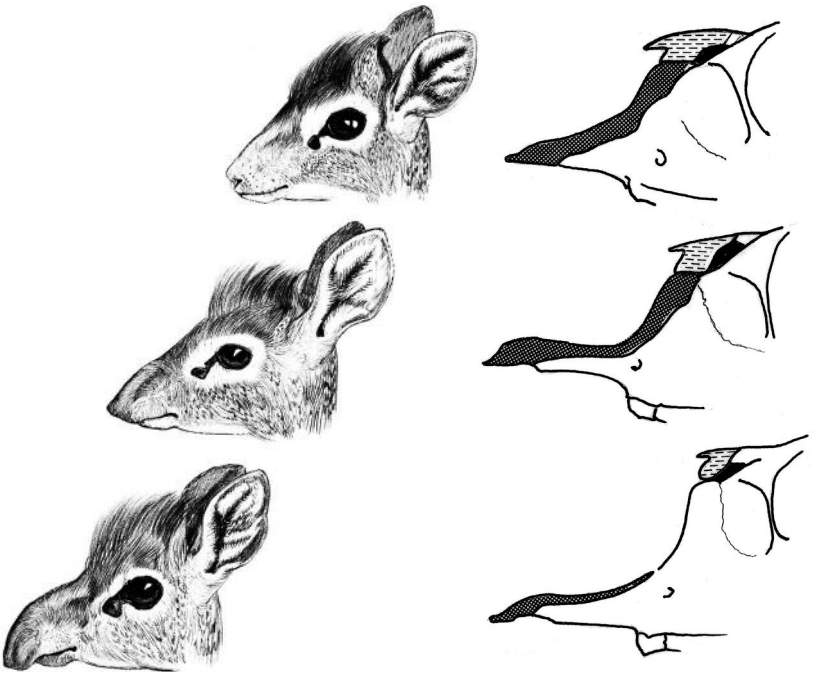
RECOGNITION Very small, long-legged antelopes with a fine, soft, grizzled (sometimes colourful) coat. They have relatively large eyes and ears, a prominent crest and a fur-covered nose that extends into a proboscis in several species. Probosces are the visible sign of a technique of temperature control that is more developed in dikdiks than in any other antelope. The nose of each species shows a different degree of elaboration and specialisation. The tail is vestigial but the pale underfur of the buttocks can be fanned into discs that are more conspicuous than any tail signal.

GENEALOGY Dikdik fossils are only known for some 4 million years (possibly 7 million years) but are likely to have begun as a distinct lineage (in the Horn of Africa) at a much earlier date. The distribution of living forms is some guide to the progress of evolution. Thus, the most conservative, least specialised forms, notably Salt's Dikdik, remain confined to the evergreen thickets that fringe the Ethiopian plateau and the Somali coast. The most advanced and most heat-tolerant species lives in the driest deserts and subdeserts of the region. Intermediate types, of the *M. kirkii* complex, occupy a much broader range of habitats in East and SW Africa.

GEOGRAPHY Essentially a group of small, arid-adapted antelopes endemic to the Horn of Africa, with a single outlying and isolated population in SW Africa. An arid corridor has clearly connected the two regions many times in the past, as is clear from other organisms with a similar pattern of



Tentative phylogenetic tree for *Madoqua* radiation (adapted from Hernández Fernández & Vrba 2005).



Left, top to bottom: Salt's Dikdik; Kirk's Dikdik; Günther's Dikdik.
Right, top to bottom: Diagram of nasals and premaxilla in the same three species.

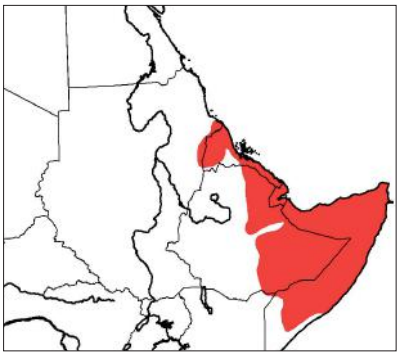
distribution. Although Kirk's Dikdik lives under a wide range of conditions in East Africa, its relative in Namibia is confined to warmer areas with less than 500mm annual rainfall.

ECOLOGY The more primitive species minimise the effects of high temperatures by being very largely nocturnal. The long-nosed Günther's Dikdik, with the greatest tolerance of heat, is more diurnal. All species depend upon low-level thickets and succulents growing on well-drained soils where there is little grass growth. If local changes allow patches of dense, tall grass to colonise their home-ranges, animals shift to another area.

NATURAL HISTORY Dung, urine and face-gland deposits are the boundaries, landmarks and focal centres for all social life. In the absence of scent marks (e.g. in a new area), all ages and sexes become alert and begin to seek or make them. While the male is the principal marker and defender of an area, his movements are entirely subordinate to those of the female – in a real sense *he* marks *her* territory. Territories may vary in size from 0.3 to 35ha. Densities range from 5 to 20 per km^2. Territories generally contain a mosaic of dense and more open ground with 6–13 stations where several dung and urine latrines are visited regularly. Where these are on a boundary two families may contribute, each sticking to its own side of the dung-marked border. Females and young contribute but males always scratch and superimpose their own contribution.

While many disturbances evoke a crouching or a creeping departure, any sudden flight tends to elicit breathy whistles from both partners in a territory, sometimes in a duet. Reunions involve face-rubbing in which females may lick the males' preorbital glands (which flow in response to excitement). Flight is usually short but very swift (up to 42kph has been recorded).

ADAPTATIONS The flexible proboscis is lined with numerous blood vessels in the mucus membrane. These are cooled by increasing the normal breathing rate from one to nearly eight breaths per second. The cooled blood returns to the heart via a sinus where hot blood going to the brain is cooled in a form of 'radiator' or *rete mirabile*. Selective cooling allows general body temperature to rise without risking brain function.



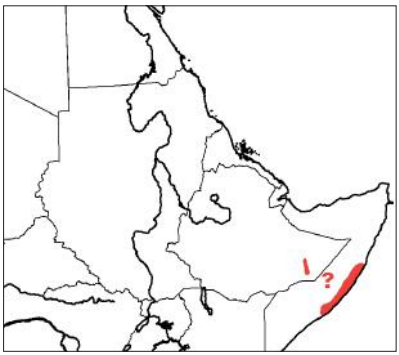
Salt's Dikdik

SALT'S DIKDIK *Madoqua saltiana*

OTHER NAMES Fr. *Dik-dik de Salt*. Ger. *Eritrea-Dikdik*.
MEASUREMENTS HB 520–670mm. T 30–45mm. Sh. ht 330–405mm. W 2.5–4.0kg.
RECOGNITION A small antelope with a short, squared-off, furry nose. Short male horns are up to 90mm. The coat is agouti-freckled and the legs sandy or reddish. There are five regional forms: two are dull-coloured (Salt's and Swayne's), two are very brightly coloured (Phillips' and Lawrence's), and one (the Harar Dikdik) is dark and somewhat intermediate. This is possibly best viewed as a superspecies but awaits further definition.
GEOGRAPHIC VARIATION (some may be full species) *M. s. saltiana* (Eritrea): reddish-grey back, large. *M. s. swaynei* (Web–Juba valleys): brown-grey back. *M. s. hararensis* (Harerge): gingery back, dark-red flanks. *M. s. phillipsi* (Gulf coast): grey back, orange flanks. *M. s. lawrencei* (Obbia coast): silver back, russet flanks.
HABITAT Evergreen and semi-deciduous bushlands and thickets in the Horn of Africa from Suakin and Hadendowa (SE Sudan) to the mouth of the R. Juba. Predominantly a nocturnal and crepuscular species, lying up in dense shade during the day. Predation must be the main factor suppressing bright colours in the western part of their range. Colours appear to correspond with colour-coding for aggressive and submissive gestures. Subordinates (of both sexes) lower their forequarters and expose their greyer backs. Dominant animals flare their red or yellow crests and strut in high-stepping, side-on displays of the red or yellow limbs and flanks.
FOOD Herbs, foliage and shoots, especially *Acacia*, browsed close to ground level.
STATUS Numbers have decreased in densely settled areas but are otherwise probably little changed. Not endangered overall.

SILVER DIKDIK *Madoqua piacentinii*

OTHER NAMES Piacentini's Dikdik. Fr. *Dik-dik argenté*. Ger. *Piacentini Dikdik*.
MEASUREMENTS HB 450–500mm. T (est.) 30–40mm. Sh. ht 300–330mm. W (est.) 2–3kg.
RECOGNITION The smallest dikdik, with very soft, fine fur and a distinctive black border to the ears. The back and sides are a uniform silvery grizzle, particularly fine on the neck and haunches. Limbs, ears and muzzle are sandy ochre, cheeks and crest are creamy yellow and the bridge of the nose is often a vivid russet.
HABITAT Shared with Lawrence's Dikdik (an eastern representative of the *M. saltiana* complex). This is possibly the most primitive and least arid-adapted of dikdiks. It inhabits very low, dense thickets growing along the Obbia coastal littoral on fertile, sandy soils



Silver Dikdik

under a powerful offshore wind. This specialised wind-shaped, sand-blasted community has year-long, low-level green growth, partly due to the sea's cooling and moisturising effect.

FOOD Shoots and foliage of shrubs and herbs in undergrowth of the Obbia littoral thicket.

STATUS The Silver Dikdik is hunted with nets and is without formal protection within its very restricted range. Its long-term survival (and that of many other endemics) must depend on conservation areas being established in this unique ecological zone.

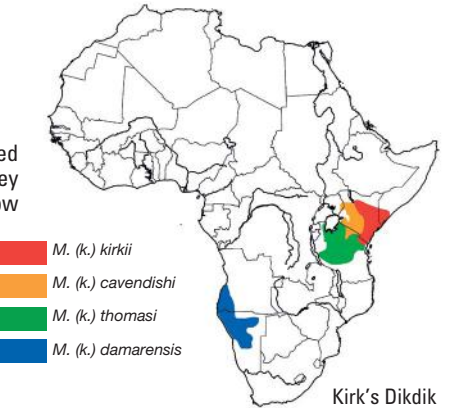
Silver Dikdik

KIRK'S DIKDIK *Madoqua (kirkii)* (4 species)

OTHER NAMES Fr. *Dik-dik de Kirk*. Ger. *Kirkdikdik*. Swah. *Suguya, Digidigi*.

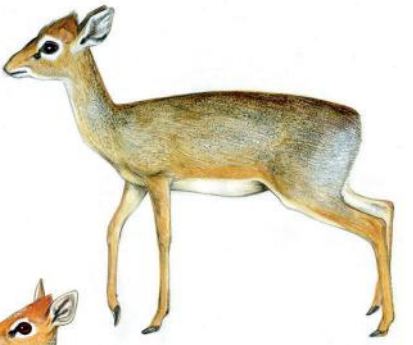
MEASUREMENTS HB 550–720mm. T 40–60mm. Sh. ht 350–450mm. W 3.8–7.2kg.

RECOGNITION A group of very slender, small-snouted antelopes with grizzled or salt-and-pepper grey coats more or less suffused with warm red or yellow ochre tints. Face, coronal crest and legs are tawny while the eye is bordered with white; ear lining, chin and belly are also white. Sharp, corrugated male horns grow to 100mm. In spite



Kirk's Dikdik

Kirk's Dikdik *M. (k.) kirkii*



Naivasha Dikdik *M. (k.) cavendishi*

Damara Dikdik *M. (k.) damarensis*

Ugogo Dikdik *M. (k.) thomasi*

of close external resemblances, each species has different numbers of chromosomes and cannot produce fertile offspring.

GEOGRAPHIC VARIATION There are four well-demarcated species:

Kirk's Dikdik, *M. (k.) kirkii* (Somali/Kenya coast and lowlands to foot of Pare/Usambara Mts): 47 chromosomes in males.

Naivasha Dikdik (Cavendish's Dikdik), *M. (k.) cavendishi* (uplands from E Uganda to Mbulu): 46 chromosomes.

Ugogo Dikdik (Thomas's Dikdik), *M. (k.) thomasi* (central Tanzania bushlands and thickets).

Damara Dikdik, *M. (k.) damarensis* (SW Africa): specialised hooves without pedal glands.

HABITAT A very wide range of habitats but with distinct geographic and ecological subtypes. Superficial resemblances were formerly interpreted as a sign of relatively recent dispersal. Contemporary molecular studies indicate an older and subtler adaptation of these dikdiks over their very wide and scattered range.

In Namibia they favour very dense thickets on hard, stony ground and limestone pavements. In Tanzania (Ugogo Dikdik) thickets dominated by *Grewia*, *Baphia* and *Pseudopropsis* are typical habitat. In the E African highlands (Naivasha Dikdik) the commonest bush is an olive (*Olea*) while the main thicket shrubs are *Aspilaia*, *Tinnaea*, *Turraea* and *Psiadia*, with *Sansevieria* and aloes being favourite retreats. In the hot, flat lowlands, north-east of these cooler uplands (Kirk's Dikdik), the vegetation is again different, with many more acacias, *Indigofera*, *Duosperma* and *Boswellia*. Thus, these dikdiks inhabit regions that have few major physical barriers but which are very distinct in flora, soils, altitude, temperatures and rainfall pattern. In combination these may serve to keep adjacent populations genetically distinct (yet, in Samburu, *M. (k.) kirki* lives within sight of *M. (k.) cavendishi* with, apparently, no hybrids (a situation that begs further study).

These dikdiks are both diurnal and nocturnal (especially active during full moon) and have similar habits to other dikdiks, including a tendency to add their dung to any new, strong-smelling intrusion into their territory. A tendency to sprinkle elephant dung with their own minuscule pellets has an amusing bite in one local folk tale. This tells that the dikdik, on stumbling over an elephant bolus, keeps piling up his own pellets in the hope that one day he will trip up the elephant.

Males are also persistent whistlers. When whistling is initiated by the approach of a dog or Leopard its immediate effects are to cause females and young to hide. The whistles also serve to distract or 'mob' the predator and to broadcast an alarm. Another important, delayed effect is social cohesion. Once the danger has past female and male invariably join up, with much nuzzling and scent-marking.

FOOD It browses evergreen shoots and foliage of the herbs, shrubs and succulents typical of each region.

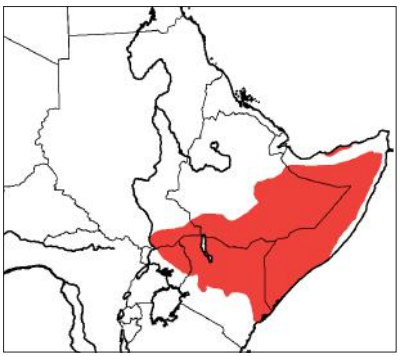
STATUS Although exterminated in many localities (as a result of agriculture, hunting and dogs), all types remain widespread and common.

GÜNTHER'S DIKDIK *Madoqua guentheri*

OTHER NAMES Fr. *Dik-dik de Günther*. Ger. *Güntherdikdik*. Swah. *Digidigi ya pua murefu*.

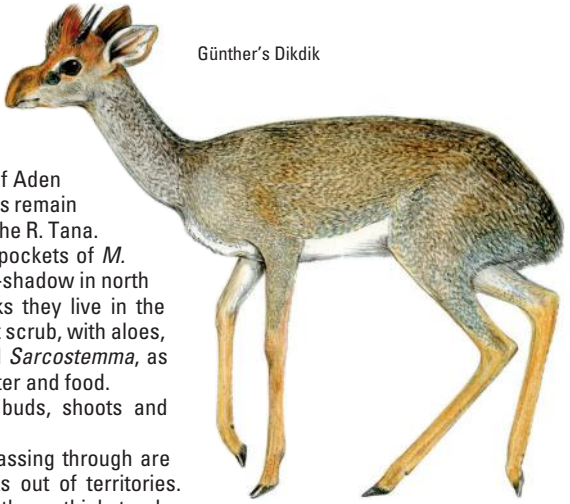
MEASUREMENTS HB 550–650mm. T 30–50mm. Sh. ht 340–380mm. W 3.2–5.5kg.

RECOGNITION A small, slender antelope, similar in colour to the Naivasha Dikdik, i.e. grizzled grey with brown or reddish flushes on sides and neck, reddish-fawn legs, nose and back of ears. Belly, chin, fur in the ear and around the eye are white. The nose is appreciably longer and more elastic than any other dikdik. In general the premaxilla and nasals are very reduced but even here intermediate skulls of both *kirkii* and *guentheri* sometimes make identification difficult. Hybrids have been bred in captivity (and might occur in the wild) but are known to be sterile. Intermediate forms make all documentation of Günther's and Kirk's Dikdiks provisional. Molecular studies have revealed that this species can have 48 or 50 diploid chromosomes and that crosses produce offspring with 49 chromosomes that are themselves fully fertile.



Günther's Dikdik

GEOGRAPHIC VARIATION (*M. g. wroughtoni*, *hodsoni*, *smithi*.) Variation and confusion with *kirkii* types makes subdivision premature.
HABITAT Distribution centres on L. Turkana, reaching the Nile at Mongalla and possibly the Gulf of Aden at Maydh. South-eastern boundaries remain uncertain but possibly bounded by the R. Tana. However, it remains possible that pockets of *M. guentheri* occur along the arid rain-shadow in north and central Tanzania. Of all dikdiks they live in the driest, hottest desert and subdesert scrub, with aloes, *Euphorbia*, *Sansevieria*, *Cissus* and *Sarcostemma*, as well as *Acacia*, providing both shelter and food.
FOOD Green (and wilted) foliage, buds, shoots and bark of dwarf shrubs and herbs.
STATUS Large herds of livestock passing through are known to temporarily force dikdiks out of territories. These dikdiks survive well in dense, thorny thickets where livestock are less able to overbrowse. Very widespread and not endangered.


Günther's Dikdik

GAZELLINE ANTELOPES Antilopini

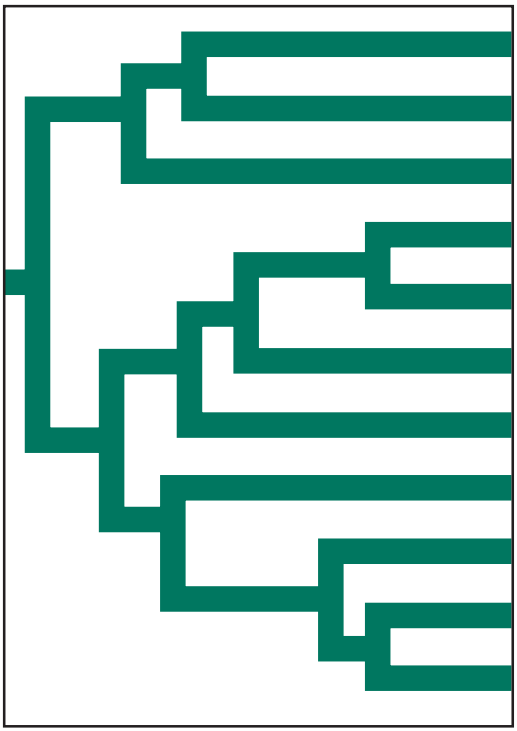
Gazelles	
Slender gazelles	*Gazella* (4 species)
Ring-horned gazelles	*Eudorcas* (4 species)
Greater gazelles	*Nanger* (5 species)
Dibatag	*Ammodorcas clarkei*
Gerenuk	*Litocranius walleri*
Springbok	*Antidorcas marsupialis*

Long-legged, long-necked antelopes with light-coloured coats, large, sensitive eyes and ears, a small mouth and, in the smaller species, preorbital glands. In dentition and skull structure they greatly resemble enlarged dwarf antelopes.

Fossils attributable to this group date back to between 12 and 15 mya in both East and North Africa. In basic tooth structure they show surprisingly little change since that time.
This is one of the few antelope groups that have been outstandingly successful outside Africa; they are spread across an arc from North and NE Africa through Arabia to arid Asia. A major factor influencing their success in this region must have been their tolerance of heat and ability to extract adequate moisture from their diet. All rely on high-quality, protein-rich diets (and this limits how large they can get in very impoverished habitats).

All are exceptionally alert to both sound and movement. In most species males are territorial while females and non-reproductive males are mobile, with individuals coming and going, assembling and dispersing without difficulty. In richer environments they remain tied to a resident home-range but for the most part they are nomadic over large areas.

The temperature regulation device typical of dry-country dwarfs (such as the dikdiks and Beira) has been taken still further in many gazellines. They too have increased the flexibility of their noses (to improve their performance as blood-cooling bellows) by freeing them from the constriction of a bony nasal tube. In *G. spekei* its nasal balloon serves as both sonic amplifier and visual flag. The antilopine trend of lengthening limbs and necks has been carried to extremes in the Giraffe-like Gerenuk, *Litocranius*, and Dibitag, *Ammodorcas*. What may have begun as an aid to greater mobility and speed in these species became a means of reaching more elevated sources of food.

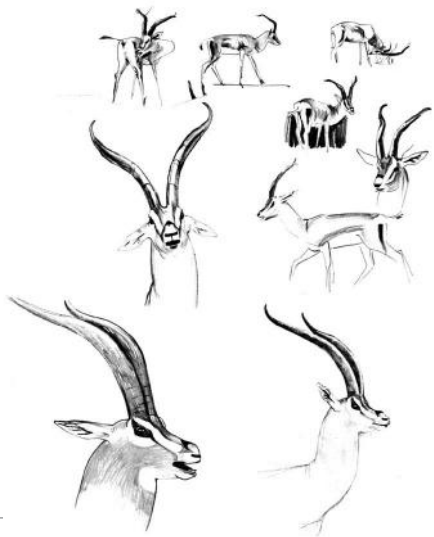


Tentative phylogenetic tree of Antilopini (modified after Hassanin *et al.* 2012).

In spite of all these innovations, the diets, teeth, stomach structures and brains of antilopines have remained very conservative.

GAZELLES *Gazella*, *Eudorcas* and *Nanger*

Slender gazelles	*Gazella*
Dorcas Gazelle	*G. dorcas*
Speke's Gazelle	*G. spekei*
Cuvier's Gazelle	*G. cuvieri*
Rhim Gazelle	*G. leptoceros*
Ring-horned gazelles	*Eudorcas*
Red-fronted Gazelle	*E. rufifrons*
Thomson's Gazelle	*E. thomsoni*
Eritrean Gazelle	*E. tilonura*
Mongalla Gazelle	*E. albonotata*
Greater gazelles	*Nanger*
Grant's Gazelle	*N. granti*
Tana Gazelle	*N. petersi*
Bright's Gazelle	*N. notata*
Soemmerring's Gazelle	*N. soemmerringi*
Dama Gazelle	*N. dama*



Field sketches of a gazelle (*Nanger (granti) granti*).

RECOGNITION Very slender, fawn or rufous antelopes; often with a dark flank-mark separating the body colour from the white underparts. A pale brow-streak runs from eye to nose, with a dark stripe below. Glands, sometimes vestigial, occur on the face, in the groin and between the toes. The tail is very short.

GENEALOGY Very ancient antelopes (at least 10 million years) that partly owe their diversity to emigration back and forth between Africa and Eurasia. The Palaearctic branch, having adapted to much colder conditions in Asia, reinvaded Africa (probably during Ice Ages) to colonise some marginally cooler niches in North Africa.

GEOGRAPHY Restricted to North and NE Africa, Arabia and India, with the sand gazelles distributed as far as China.

ECOLOGY The four groups represent four adaptive trends. The *dorcas* group are small desert gazelles. The *rufifrons* group are small gleaners adapted to less arid but very open steppes around the margins of the Sahara proper. The Palaearctic *leptoceros* group are cold-adapted species. The *Nanger* gazelles are large, desert gazelles (in East Africa they have maintained occupation of benign habitats that were formerly drier).

NATURAL HISTORY Horns and horn shapes are influenced by population density because frequent fighting selects for stronger weapons and more effective defence. Thus Grant's Gazelle (more consistently numerous and densely distributed) has the longest and heaviest horns (up to 800mm.) The Saharan Dama Gazelle normally lives at low densities and has horns half this length. Soemmering's Gazelle, between the two extremes, has horn lengths of up to 580mm.

At an early stage in their evolution gazelles would have combined their ecological shift into more open habitats with a behavioural change towards visual rather than olfactory or vocal signals. As a result most species are highly conspicuous, with prominent signal patches (usually white) on head, rump, flanks and feet. All gazelles flag their head, posture, wag their tail, shudder their flanks, bounce, leap or race around. All are messages intended for other gazelles. Conspicuousness, in turn, has reinforced their dependence upon open country (where they normally have adequate warning of the approach of predators). Only as fawns do gazelles hide like the dwarf antelopes, with which they share a common ancestry.

ADAPTATIONS Heat tolerance in desert gazelles is achieved through a refinement of the nasal blood-cooling found in dikdiks. The less arid-adapted rufous gazelles are more wasteful of water, using conventional panting to cool down. Desert gazelles accumulate adequate moisture by feeding on dew-soaked vegetation late at night.

DORCAS GAZELLE *Gazella dorcas*

OTHER NAMES Fr. *Gazelle dorcas*. Ger. Dorkasgazelle.
MEASUREMENTS HB 900–1,100mm. T 150–200mm. Sh. ht 550–650mm. W 15–20kg.

RECOGNITION The smallest gazelle but proportionally the longest limbed, with small, fine hooves. It is notable for its very long ears. Horns, on both sexes, are long (up to 380mm), with up to 25 annular rings, and lyre-shaped (out then in at the tips). Colour is light fawn with poorly differentiated flank stripes but light and dark streaks down the face.

GEOGRAPHIC VARIATION *G. d. dorcas* (E Sahara), *G. d. massaesyla* (W Sahara), *G. d. isabella* (east of the R. Nile), *G. d. beccarii* (Eritrean uplands), *G. d. pelzelni* (N Somali coast).

Dorcas Gazelle

HABITAT North and NE Africa in driest subdeserts, mainly on stony or compacted soils with very sparse vegetation. Resident animals tend to disperse in small parties but converge on localised resources in larger numbers. When nomadic, they may aggregate in herds of up to 100. They are fecund, with a 6-month gestation. Sexually mature in 18 months, they live for more than 12 years.

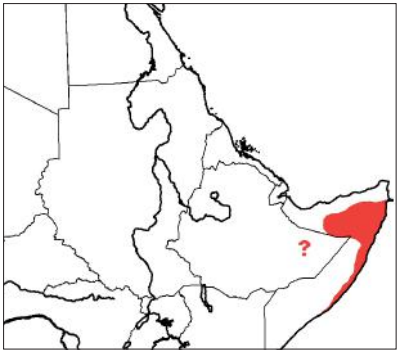
FOOD Herbs (notably *Chrozophora*), succulents and, especially during the driest periods, shoots of shrubs such as *Acacia*, *Maerua* and *Leptadenia*. Dorcas Gazelles are mainly active at night and around dawn and dusk.

Dorcas Gazelles

STATUS Endangered or exterminated in many localities but still widespread over much of its range. Not endangered overall.

SPEKE'S GAZELLE *Gazella spekei*

OTHER NAMES Fr. *Gazelle de Speke*.
Ger. *Spekegazelle*.
MEASUREMENTS HB 950–1,050mm. T 150–200mm. Sh. ht 500–600mm. W 15–25kg.
RECOGNITION A rather small gazelle with an inflatable nasal region just behind the nostrils. It is fawn with a crisp black flank stripe (and paler band above it), white buttocks with dark margins, a pale face and undulating horns with broad annulations.
HABITAT The Indian Ocean littoral of Somalia in stony semi-desert dominated by stunted succulents,



Speke's Gazelle

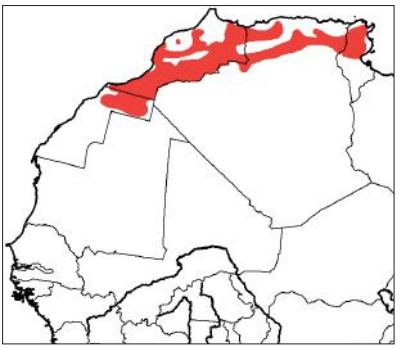
Speke's Gazelle male with nasal sac inflated.

aloes, shrubs and sparse desert grasses (*Panicum* and *Eragrostis*). The centre of its range is the Nogal Valley where small groups, occasionally numbering up to 20, gather or disperse in response to the sparse vegetation. It is notable for a loud sneeze, said to be an alarm call (probably as much an advertisement of status), that is made by inflating and emptying the nasal sac, which is such a prominent feature of this species.

FOOD Grass, herbs, shrubs and succulents.

STATUS Still widespread, although intense competition from livestock may have reduced numbers in some areas. Not endangered.

CUVIER'S GAZELLE *Gazella cuvieri*



Cuvier's Gazelle

OTHER NAMES Atlas Gazelle, Edmi Gazelle. Fr. *Edmi*. Ger. *Echtgazelle*.

MEASUREMENTS HB 950–1,050mm. T 150–200mm. Sh. ht 600–690mm. W 15–20kg (♀); 20–35kg (♂).

RECOGNITION A tallish grey-brown gazelle with broad, lighter and darker bands across the flanks, a white belly and buttocks, and a black tail. The top of the nose has a prominent black spot. The face is well striped and the ears are pale, long and narrow. Horns are long (250–370mm) and well formed in both sexes; strongly annulated, they rise vertically before diverging out and back; the smooth tips curving in and forwards.

HABITAT From Morocco to Algeria (formerly to Tunisia) in maquis scrub mosaics, open parkland of pines (*Pinus halappensis*) evergreen oak thickets and patches of rushes (*Juncus*). It favours both stony and sandy ground on hills and plateaus. Here it lives in widely spaced territories where males attend one or more females and their young. It is rarely seen in groups of more than eight. Mating takes place in early winter with births in the spring (April–May).

FOOD Grass, herbs and shrubs; often visits cultivated fields.

STATUS Rare and now scattered in a decreasing number of localities, Cuvier's Gazelle is protected in a few reserves. Because it is heavily poached and suffers continuing habitat degradation, mainly from overgrazing by livestock, it is in danger of extinction.

RHIM GAZELLE *Gazella leptoceros*

OTHER NAMES Slender-horned Gazelle, Loder's Gazelle. Fr. *Rhim*. Ger. *Dünengazelle*.

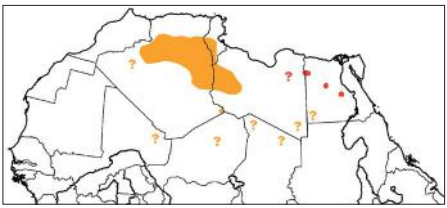
MEASUREMENTS HB 1.0–1.1m. T 150–200mm. Sh. ht 650–720mm. W (est.) 14–18kg.

RECOGNITION A medium-sized gazelle of very pale yellowish-grey colour, only faintly marked with face and flank stripes. The ears are long and narrow. Horns (appreciably thicker and longer in males) are long and nearly straight, with 20–25 well-defined annulated rings. Outer hooves are broader than the inner ones.

GEOGRAPHIC VARIATION Eastern Rhim *G. l. leptoceros*; Western Rhim *G. l. loderi* (validity uncertain).

HABITAT Strictly confined to the great sand deserts, or ergs, of the E Sahara from Algeria to Egypt. Here it lives among the dunes in very small parties, usually a male with one or more females and their young.

FOOD Main grass reported to be a feather grass (*Aristida pungens*, or 'drinn'); also foliage of *Acacia raddiana*, fruit of *Colocynthis* and the halophytes *Nitraria* and *Anabasis*, as well as succulents, herbs



G. l. leptoceros
G. l. loderi
(a very provisional subspecies)

Rhim Gazelle

Rhim Gazelle

and foliage of scarce shrubs. The Rhim Gazelle feeds at night and in the early morning. Water requirements are drawn solely from moisture in its food.

STATUS In spite of its remoteness, the Rhim Gazelle has been a traditional quarry for mounted (and now motorised) hunters and its horns used to be sold as ornaments in N African markets and shops. Known to be rare, possibly endangered. Precise status not known.

RED-FRONTED GAZELLE

Eudorcas rufifrons

OTHER NAMES Fr. *Gazelle à front rouge*. Ger. *Rotstirngazelle*.

MEASUREMENTS HB 800–1,200mm. T 150–270mm. Sh. ht 550–820mm. W 15–25kg (♀); 20–35kg (♂).

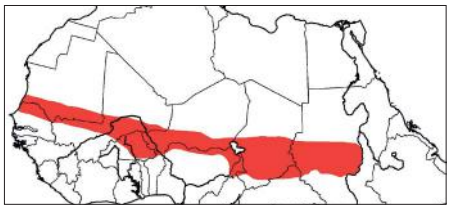
RECOGNITION An elegant gazelle with a warm reddish back and white underparts separated by a black flank band. The white buttocks contrast strongly with the deep russet colour on the back which extends to the root of the all-black tail. The face is white with red or brown stripes, the ears are narrow and pointed. The double-arched horns have numerous annulations.

GEOGRAPHIC VARIATION Red-fronted Gazelle: *G. r. rufifrons* (W Sahel), *G. r. laevipes* (E Sahel), *G. r. kanuri* (South of L. Chad). Red Gazelle – *G. r. rufina*? (Algeria – extinct).

HABITAT They prefer dry steppes and *Acacia/Combretum/Lannea* shrublands of the Sahel. Migratory animals, they form, fragment and reform easily. In Waza NP densities of 0.5–2.5 per km^2

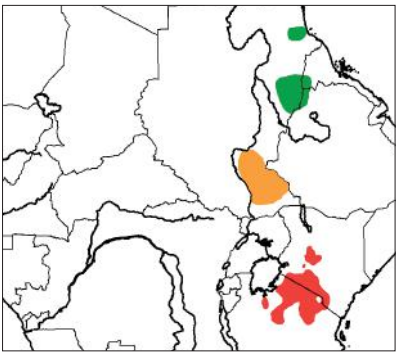
FOOD Growing green grass in rains; switches to herbs and foliage of *Acacia*, *Balanites* and *Boscia* in the dry season.

STATUS Once widespread throughout their range, Red-fronted Gazelles now occur in fragmented and declining patches. Not endangered overall.



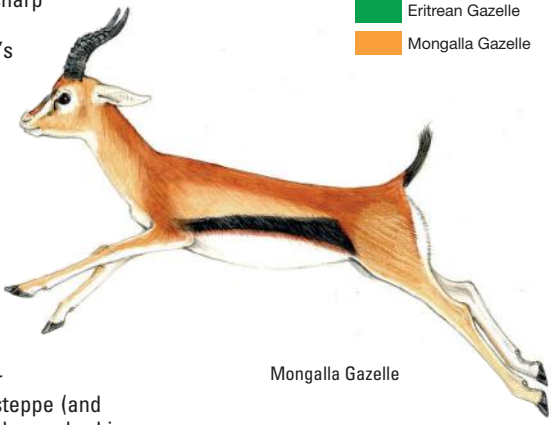
Red-fronted Gazelle

THOMSON'S GAZELLE *Eudorcas thomsoni*, ERITREAN GAZELLE *Eudorcas tilonura* and MONGALLA GAZELLE *Eudorcas albonotata*



OTHER NAMES Fr. *Gazelle de Thomson*. Ger. *Thomsongazelle*. Swah. *Swala tomi*.
MEASUREMENTS HB 800–1,200mm. T 150–270mm. H 550–820mm. W 15–25kg (♀); 20–35kg (♂).
RECOGNITION A compact little gazelle with a warm sandy back and white underparts separated by a bold black flank band. The white buttocks have black marginal stripes and the colour on the back extends to the root of the all-black tail. The face is boldly striped (with much individual variation) and the ears are of moderate length. The mildly undulating horns have numerous sharp corrugations.
GEOGRAPHIC VARIATION The Thomson's Gazelle group now comprises three species:
Thomson's Gazelle *E. thomsoni* (L. Victoria/Eastern Rift Valley region);
Eritrean Gazelle (Heuglin's Gazelle) *E. tilonura* (E Sudan and W Eritrea);
Mongalla Gazelle *E. albonotata* (Sudd region of SE South Sudan, east of the Nile).
HABITAT The dry grasslands and shrubland habitats in E Africa. They prefer heavily grazed, trampled or burnt grasslands or naturally open steppe (and stay on pastures long deserted by larger herbivores as long as some miniature growth remains). Socially they are exceptionally flexible. They are migratory animals, without lasting ties between individuals, spread out in a loose mosaic of overlapping female herds. Each individual shares with many others a particular home-range within which activities such as going to water (treks of 15km are not unusual), resting and moving to fresh pasture are often coordinated. Such temporary associations among a large number (up to 100 or more) suggest that, in spite of their individual independence, each gazelle knows and remembers a large number of 'friends', 'clan' members or other relatives. Males are less flexible and mature individuals fight to hold and defend territories within the females' favourite pastures. When resources are exhausted only thirst or hunger drives them away. Solitary territorial males in an empty landscape are a common sight.

This species retains active preorbital glands and males mark grass stems and twigs at preferred spots (often hillocks or compacted bare patches).



Mongalla Gazelle

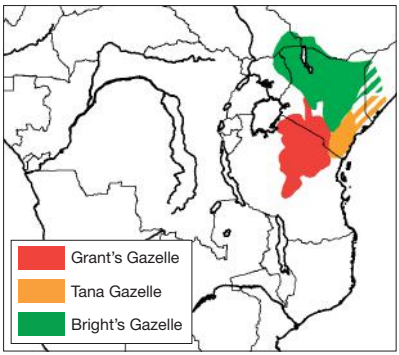
Thomson's Gazelle

They also drop dung at these places. Frequent fights and stand-offs help maintain boundaries between neighbours. Males attempt a mild, ineffectual 'herding' of females in order to delay their departure but their primary interest is in finding oestrous females to mate with.

FOOD Mainly growing grass in the wet season but switches to herbs, the foliage of shrubs and seeds of *Acacia*, *Balanites*, *Sida* and *Solanum* in the dry season. *Themeda*, *Cynodon* and *Harpachne* are preferred grasses in Kenya.

STATUS All populations are declining but are still locally common at reduced densities. In some areas their status is unchanged, but *E. tilonura* is now rare. Not endangered overall.

Grant's Gazelle



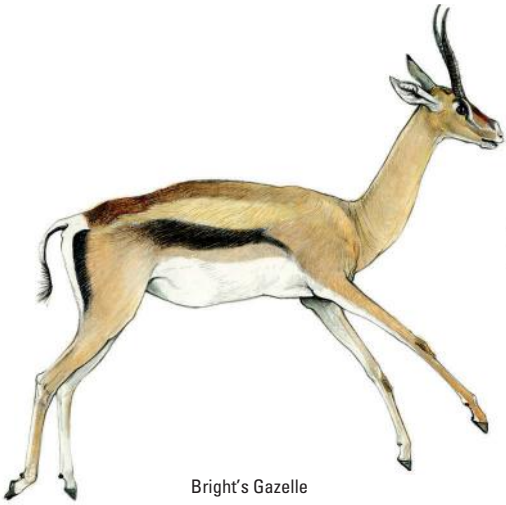
Nanger (granti) species group

GRANT'S GAZELLE *Nanger (granti) granti*, TANA GAZELLE *Nanger (granti) petersi* and BRIGHT'S GAZELLE *Nanger (granti) notata*

OTHER NAMES Fr. *Gazelle de Grant*. Ger. *Grantgazelle*. Swah. *Swala granti*.

MEASUREMENTS HB 1.4–1.6m. T 200–280mm. Sh. ht 780–830mm (♀), 850–910mm (♂). W 38–67kg (♀), 60.0–81.5kg (♂).

RECOGNITION Large, pale gazelles with upright stems to the long horns above relatively small eyes, which are set in characteristic, leaf-shaped eye patches,



Bright's Gazelle

Tana Gazelle

or 'masks', of jet-black skin and hair incorporating vestigial preorbital glands. Above the nostrils there is a slightly inflatable nasal sac. The tail is markedly tapered and carries a wispy fringe. There are hoof and knee glands. The root of the tail is white, extending the buttock patch into a bold white configuration (the rectangularity of which is emphasised by a dark vertical stripe down each thigh). Colour varies individually, especially on the flanks, but with distinct regional trends. Thus, females often have dark flank stripes, but less often in the north-east, while the flanks of males are also dark only around L. Turkana. Horns also vary individually and regionally (500–800mm). Male horns west of L. Eyassi and L. Natron tend to splay at a sharp angle, with downward curls at the tip. North of Mt Kenya horns tend to be more parallel.

Some ten forms have been described; the most distinctive being the Tana, or Peters's, Gazelle, *N. petersi*, which has a back that is fawn-brown from neck to tail, with a white buttock patch reaching only to the anus. Overall proportions are smaller. Facial stripes are faded. The horns are almost straight.

GEOGRAPHIC VARIATION The Grant's Gazelle group now comprises three species:
Grant's gazelle, *N. (g.) granti* (S Kenya and N Tanzania, from Mt Kenya to Ruaha valley);
Tana Gazelle, *N. (g.) petersi* (lower Tana valley);
Bright's Gazelle, *N. (g.) notata* (NE Uganda, S Ethiopia, N Kenya [north of Mt Kenya] and S Somalia).

HABITAT This species group could be called 'Rift Valley gazelles' because their distribution spills over from the central axis or 'spine' of the East Rift. This upland distribution coincides with rain-shadows and with an arid corridor of unstable climate across the East African plateau that is known to have been very much more arid in the past. The Tana species lives in the lower Tana valley, Lorian swamp, Wajir and the Dheere-Madheeri depressions (west of the R. Juba in Somalia). Here the gazelles live on very flat plains that are briefly flooded during occasional and unpredictable rains (when they do flood it tends to be in April or December). Where their range becomes dense bush the gazelles are restricted to glades or open, scrubby valleys. However, in the 1950s elephants became so numerous in Tsavo that they cleared large areas of woody growth (a clearance extended recently by charcoal-burners) and the Tana Gazelles expanded west and south, meeting up with *N. (g.) granti* across a broad front south of the Galana valley. Where conditions suit them all year, both sexes are resident, the males on midden-marked territories of 8ha to 10km^2, the females circulating over still larger areas. Elsewhere, seasonal movements take them from higher, well-drained areas during the rains out onto flat, grassy valleys in the dry season. They do not tolerate soft soils but will live in bush and tall grass more readily than any other gazelle (but only seasonally). Fighting and territorial displays, characterised by flicking of the raised head on the bulging neck and slow, stiff circling, increase during biannual mating peaks (December and May north of the Equator). Births follow a 6-month gestation. Rainy-season births appear to take place in denser cover. The fawn remains hidden for several weeks. At this time mothers may actively attack small predators.

FOOD Herbs and shrub foliage are preferred during the later wet and dry seasons; grass is grazed only while it is young and green. The fruits of *Balanites* and *Solanum* have also been recorded. Intense grazing by other species removes grass, thereby favouring herbs and the gazelles that feed on them. Grant's Gazelle is typically found in herbivore concentration areas, such as the Serengeti plains, and are commonly seen in mixed groups. Herds of these gazelles may number up to 500 at such times.

STATUS Although eliminated in some agricultural regions and areas where poaching is uncontrolled, these gazelles are still widespread and common both within and outside national parks and reserves.

SOEMMERRING'S GAZELLE *Nanger soemmerringi*

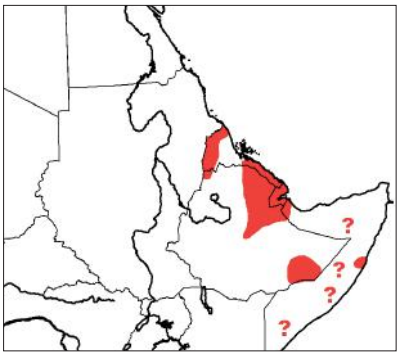
OTHER NAMES Fr. *Gazelle de Soemmerring*. Ger. *Sömmering-gazelle*.

MEASUREMENTS HB 1.25–1.5m. T 180–230mm. Sh. ht 810–900mm. W 38–46kg.

RECOGNITION A large, generally pale gazelle with extensive white on the rump, strongly marked facial blazes, a large head and heavy, short, backwardly swept horns that form a lyrate shape with in-pointed hooked tips. It is long in the leg, with big hooves and a relatively short neck. The tail, like that of other *Nanger* gazelles, is short and tapered, with a mainly white fringe of short hairs.

GEOGRAPHIC VARIATION *N. s. soemmerringi* (Sudan and Eritrea): brown face, shorter horns. *N. s. berberana* (Somalia and NE Ethiopia): black face, longer horns. *N. s. butteri* (S Ethiopia): dark flank, thigh stripes. An unnamed dwarf from Kebir I. in the Dahlak archipelago (Eritrea) has differently

Soemmerring's Gazelle



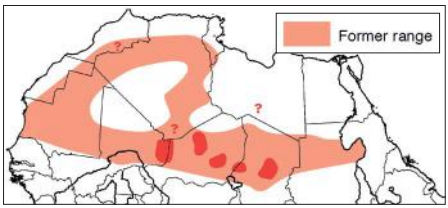
Soemmerring's Gazelle

curled horns and could be a distinct island species.

HABITAT Endemic to the Horn of Africa where they once inhabited most of Somalia and the last, lowest foothills of the Ethiopian massif on its northern and eastern faces. Here they once gathered in hundreds on open plains and made substantial seasonal migrations (notably down from the upper Atbara valley to spend the wet season on the exposed plains below Kasala). They favour rough, hilly country with scattered evergreen thickets and *Acacia*/*Commiphora* steppe, as well as open, short-grass plains. Today they are seldom seen in herds larger than about 15. These are often groups of females and their young herded by a single male on his midden-marked territory. Like Grant's Gazelle, males flick their heads during confrontations. They yank their hooked horns sideways during fights in efforts to destabilise the opponent. When tending or herding females, males make a nasal croak. A mating peak has been recorded between September and November. Gestation lasts 198 days and the young lie up for a month. They are weaned by 6 months and reach sexual maturity by 18 months. Animals live for 14 years.

STATUS Exterminated over the greater part of their range, these gazelles now exist in numerous small pockets. Although hunting may have played a significant part in this decline, overgrazing and habitat degradation by domestic stock is probably the main cause. Listed by IUCN as threatened.

DAMA GAZELLE *Nanger dama*



Dama Gazelle

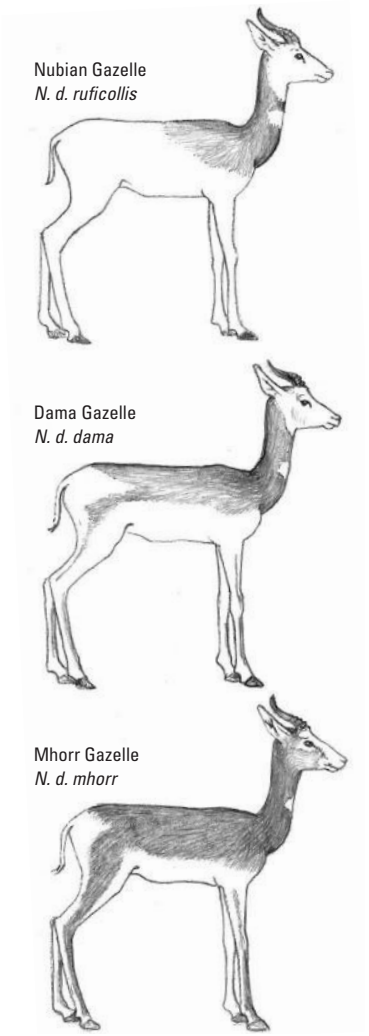
OTHER NAMES Addra Gazelle. Fr. *Gazelle dama*. Ger. *Damagazelle*.

MEASUREMENTS HB 1.40–1.65m. T 250–350mm. Sh. ht 0.9–1.2m. W 40–75kg.

RECOGNITION The largest of all gazelles, with long legs and neck, a big head and short, compact, double-curved horns. The face and underparts are white in all forms; the most westerly resemble Soemmerring's Gazelle in pattern but are a vivid rufous rather than fawn. The most easterly populations are very variable but have many individuals where the rufous element is confined to the neck and upper shoulders but are otherwise white. The tail is short and white, with a sparse fringe.

GEOGRAPHIC VARIATION Dama Gazelle, *N. d. dama* (W Sahara); Nubian Gazelle, *N. d. ruficollis* (Sahara west of the Nile). There was formerly a wide zone of very variable integration between these two. Mhorr Gazelle, *N. d. mhorr* (North Africa to Mauritania).

HABITAT Until recently one of the most widespread and common of Sahara gazelles, making mass movements between its wet-season pastures deep in the Sahara and dry-season range in



Dama Gazelle

the semi-deserts and open bushlands of the Sahel. Herds of many hundreds used to be seen on the move before dispersing into smaller groups numbering up to about 15. The principal mating peak in the Sahara was between March and June, the wettest months. Births would peak in about December, by which time the gazelles had moved well to the south so that the newborn could find shelter in the light scrub and grassland of the Sahel. Similar movements between moister and drier parts of their range took place in Morocco and Algeria. Here they travelled south into the Sahara, returning north where they preferred reg and hammada pastures. The last animals here were seen in the 1950s.

FOOD Mainly herbs, succulents and shrubs (notably *Acacia*, which the gazelles could browse above 2m by standing up on the hindlegs like a Gerenuk). These gazelles were also reported to eat coarse desert grasses. Their seasonal movements were symptomatic of their need for moisture (albeit moisture contained in browse).

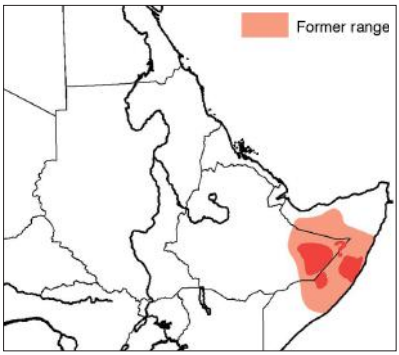
STATUS Dependence on movement into the Sahel was fatal for Dama Gazelles. Large, very conspicuous antelopes, they came into contact with ever-increasing numbers of livestock and people along almost the entire length of their range and declined very rapidly between the 1950s and 1970s. They are now extinct in Algeria, Mauritania, Senegal and Burkina Faso, nearly so in Mali, Niger and Sudan. The principal authority on wildlife in this region, J. E. Newby, wrote in 1990: 'the problems for these animals and for the people trying to conserve them have been exacerbated by a new wave of hunters invading the Sahelian countries in search of new hunting grounds'. Wealthy and irresponsible foreigners are purchasing a part in the extermination of Sahelian wildlife. Less accessible parts of this vast region may allow survival for a while but only in Chad do Dama Gazelles have a realistic hope of recovery once fighting ceases. Since 1990 the situation has worsened and the Sahara may soon be empty of all its larger endemic ungulates. Listed by IUCN as threatened with extinction.

DIBATAG *Ammodorcas clarkei*

OTHER NAMES Clarke's Gazelle. Fr. *Dibatag*. Ger. *Lamagazelle*.

MEASUREMENTS HB 1.52–1.68m. T 300–360mm. Sh. ht 800–880mm. W 22–29kg.

RECOGNITION A very tall, slender antelope with large eyes, long, black-tipped ears and a face with typical gazelline markings down an elongated but sharply tapered muzzle. The mouth, teeth and jaws are minuscule. The males have shortish horns with heavy, annulated bases and tips that are sharply angled forward. Its name means 'erect tail' in Somali and the heavily furred black tail, carried like a waggling baton, is indeed its most conspicuous feature. During flight the tail and head are carried erect which distinguishes this species from the Gerenuk, which adopts a more horizontal posture. The body colour is a uniform fawn-grey, with ochre-coloured legs and a red forehead. The undersides and brow stripe are white and the long buttock hair can be flared out into a brilliant white signal. There are preorbital glands and glandular 'brushes' below the knees.



Dibatag

DISTRIBUTION Restricted to a single vegetation type in central Somalia and the Ogaden (Ethiopia). Here it prefers areas of well-drained, sandy soils. It avoids dense thickets and very stony ground.

HABITAT A plant community called camel-brush or 'gedguwa'. This is an *Acacia/Commiphora* deciduous bushland and thicket in which important evergreens are *Boscia*, *Dobera*, *Salvadora*, *Grewia* and *Cadaba*. During and immediately after the rains it visits more open glades and in general prefers a mosaic of thickets and grassland with scattered trees.

FOOD Mainly the foliage of *Acacia* (at least six species noted), *Commiphora* and other evergreen trees and shrubs, but probably less dependent on woody growth than the Gerenuk. It has been reported to graze on herbs and new grass during the rains. Sodom apples (*Solanum*) have also been recorded in its diet. The small, mobile, very pointed but muscular lips assist the plucking of minute items, such as buds and shoots, from within dense barricades of thorns. The Dibatag can reach up into small trees and bushes by balancing on its hindlegs, keeping balance with lightly propped forelegs but this mode of feeding is thought to occur less frequently than in the Gerenuk.

BEHAVIOUR Males are territorial, visiting their latrines daily to renew the piles of small, dark, oblong pellets, but they are also reported to make periodic small-scale shifts in range. Up to five females and their young have been seen with single adult males but singles or twos are commoner. Captive males rub their facial glands on the female's rump and both sexes have been seen to nibble or lick one another's glands. Males douse their muzzles in female urine and lip-curl like all other bovids. There is a mating peak during the heavy rains in April and May.

Dibatag horn-wrestling

After 6 months' gestation a single fawn is born during the short rains (October–November) and lies up in thick bush. Young remain concealed for 2 weeks and reach sexual maturity at between 12 and 18 months. The Dibatag is thought to live for 10–12 years.

ADAPTATIONS The contrast between great height, substantial weight and extreme delicacy of mouth-parts poses special problems for fighting males. Not only must they avoid injury to the muzzle, they also risk toppling because tall, heavy animals are easily thrown off balance. Males squaring up for a fight therefore tuck their vulnerable noses between their forefeet. Their horns are sufficiently long to force them into a standing contest. Their thick, heavy napes and upper necks engage and the horns clash along their curved back surfaces. From this position, pushing hard and wrestling from the pivot of their broad napes, each animal seeks to hook his opponent off balance. This technique of fighting ensures that there is little risk to their fragile muzzles and it is the rumps of fleeing losers that are more likely to get stabbed by sharp horn tips.

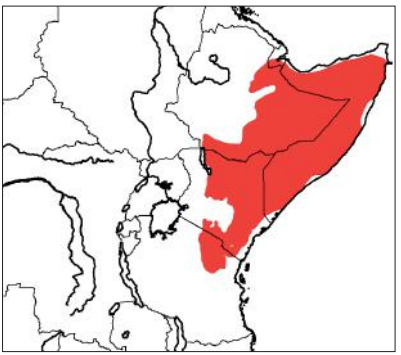
STATUS This species has lost at least half of its known recent range and probably occupies a much smaller fraction of its original area of distribution. There are two or three remaining pockets where it remains fairly common but poaching and displacement by domestic stock makes continued decline likely. Proposed conservation areas at Hobyo (Obbia), Haradere-Awale Rugno in Somalia and E Ogaden in Ethiopia must await more peaceful times to be implemented. Listed as vulnerable (IUCN).

GERENUK *Litocranius walleri*

OTHER NAMES Waller's Gazelle. Fr. *Gazelle de Waller*. Ger. *Giraffengazelle*. Swah. *Swala twiga*, *Njonga*.

MEASUREMENTS HB 1.4–1.6m. T 220–350mm. Sh. ht 0.8–1.05m. W 28–45kg (♀); 31–52kg (♂).

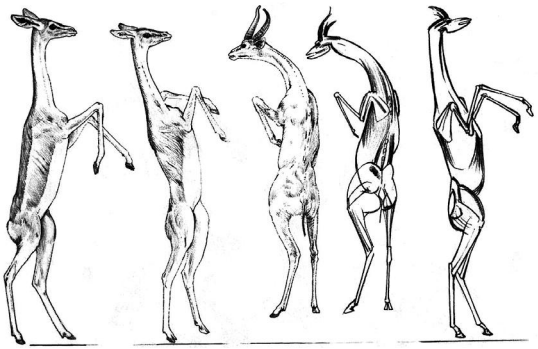
RECOGNITION A very tall, long-necked, long-eared antelope with a two-toned chestnut back, light fawn sides and white underparts. Like the Dibatag it has extremely small mouth-parts for a large antelope. The contrast is greatest in the very heavily horned male where the upper neck is thicker than its lower part and the dainty little muzzle protrudes from a heavily reinforced brain-case. The horns have thick, diverging shafts, rising in a bold arc and then curling forward in a tight hook towards the tip. It has preorbital face glands, scented brushes below the knees and glands between the hooves.



Gerenuk

female

male

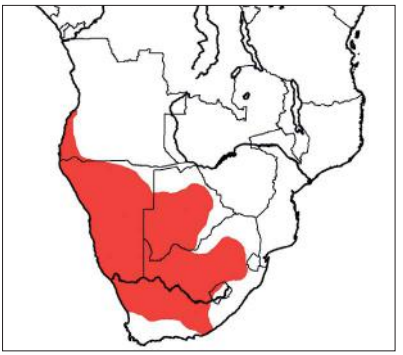


Gerenuk female and male in bipedal posture.

GEOGRAPHIC VARIATION Two ill-defined subspecies are listed, which are sometimes regarded as full species. The southern nominate race, *L. w. walleri*, has smaller cranial measurements than *L. w. sclateri* in the northern part of its range.
DISTRIBUTION The Horn of Africa extending into NE Tanzania. Mainly semi-arid bushland below 1,200m. Known to have been more widely spread in the more distant past (up the Red Sea littoral).
HABITAT Dependent on an abundance of bushes and small trees, including evergreens. It avoids true, dense thickets and is commonest on flats where *Acacia*, *Commiphora* and other bushland species are well spaced or in small clumps. It has a wider tolerance of bushland types than the Dibatag.
FOOD Almost exclusively a tree-foliage browser (creepers and vines being the main exception). *Acacias*, with their very small, nutritious leaflets, are the major staple but seasonal and regional variations follow what plants are in leaf or in bud at the time. Skunk Bush, *Premna resinosa*, is a favourite in Kenya but 87 different trees and shrubs have been recorded in the diet. The Gerenuk habitually rises on its hindlegs to reach a zone over 2m high (where Giraffes are the only, partial, competitors). Its minute, pointed muzzle can extract leaves from very thorny tangles.
BEHAVIOUR The Gerenuk is normally very residential, living in well-spaced home ranges of 3–6km^2. Here single adult males exclude other adult males but regularly associate with females and their offspring. In some cases males share exactly the same range as one or more females, regularly visiting or following them. Shifts of range are known but are probably rarer with age. Males in particular become more strictly residential with age. Males mark out their territories by inserting twigs into their preorbital glands. Unlike the Dibatag, they do not make dung middens (which in other antelope species tend to abut the ranges of other males and are often contributed to by both neighbours). It is therefore interesting that Gerenuk facial gland deposits are distributed along the borders of very small domains that do not abut those of neighbours, suggesting that males live in such large home-ranges that they can only mark core areas. It is possible that some kind of no-man's-land lies between male gerenuk territories. Among females, overlaps in range and sporadic associations (sometimes larger aggregations) hint at the existence of local 'clans' of related animals that know one another. The contact call is a frog-like humming grunt.

Like Dibatag, Gerenuk males rub their face glands on females. Occasionally they threaten them, making a low rumble (apart from a buzz of alarm they are otherwise rather silent animals). Young are born after a 7-month gestation and most births occur during the rains. The newborn is well hidden and only emerges to join its mother after several weeks. A mother may be accompanied by more than one offspring (female young become independent at about 12 months, males parting later, at up to 18 months). Animals are thought to live for 10–12 years.
ADAPTATIONS In spite of many similarities, Gerenuk and Dibatag males differ most in the shape of their horns. The Gerenuk's fighting technique differs fundamentally, as its much heavier horns, which curve in the opposite direction, are clashed together with violent downward nods of the head. Backward extension of the very hard brain-case provides the immediate leverage for the hammer-like blows exchanged by fighting males.
STATUS Although eliminated from parts of its range in East Africa, the Gerenuk is still widespread

both within and outside national parks and reserves. Not endangered overall.

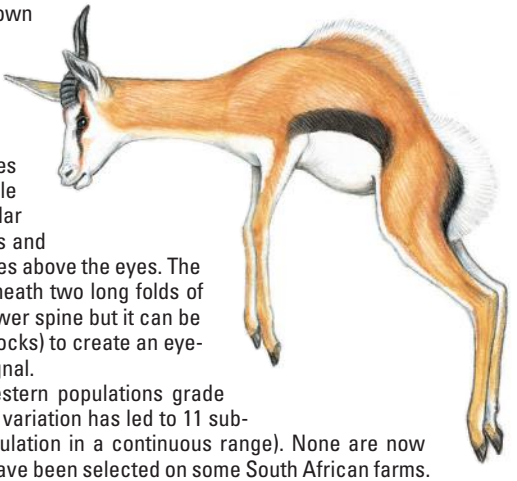


Springbok

SPRINGBOK (SPRINGBUCK)

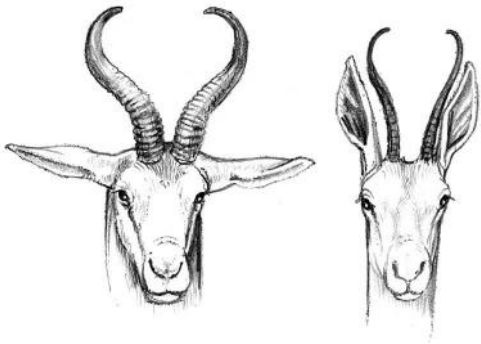
Antidorcas marsupialis

OTHER NAMES Fr. *Antidorcas*. Ger. *Springbock*.
MEASUREMENTS HB 1.2–1.5m. T 140–280mm. Sh. ht 680–900mm. W 20–43kg (♀), 30–59kg (♂).
RECOGNITION In size and general proportions the Springbok is very gazelle-like, and they share striped faces and bands on thighs and flanks. They are generally assumed to be a sort of 'southern gazelle.' However, there are several differences that distinguish them. Their white underparts extend well up the sides, rump and dorsal midline. The head is also white but marked from crown to mouth with brown streaks (which conceal the very protuberant eyes). The white ears are exceptionally long and narrow. Upperparts are cinnamon fawn above an arc of black or brown on the flanks. The Springbok differs from gazelles in having a longer, broader and less flexible bridge to the nose, deeper, more muscular cheeks, and horns that sweep backwards and hook inwards from peculiarly swollen bases above the eyes. The white dorsal crest is normally hidden beneath two long folds of scent-secreting skin that run along the lower spine but it can be erected (as can the white hair on the buttocks) to create an eye-catching, and presumably odoriferous, signal.



GEOGRAPHIC VARIATION Smaller south-western populations grade into larger north-eastern ones. Individual variation has led to 11 sub-species being named (from a single population in a continuous range). None are now considered valid. Dark and pale morphs have been selected on some South African farms.
DISTRIBUTION SW Africa, the Namib, Kalahari and Karoo deserts. This species or its immediate antecedents was once sufficiently common in East Africa to become the most frequently fossilised of all antelopes (three species found over a period of more than 2 million years).
HABITAT Dry, open plains with a marked preference for flat drainage lines and the fringes of pans where soil conditions or overgrazing keep grasses and herbs low. It lives in dry *Acacia* savannas in the Kalahari, bushy shrubland in Namibia, dwarf and grassy shrublands in the Karoo. It is exceptionally mobile, moving long distances to find scarce pastures during droughts but instantly returning to traditional and well-known localities when the rains break. Vast herds of migrating Springboks formerly earned the Afrikaner name of *treckbokken*. It avoids tall grass, thick woodland and broken ground. Pliocene fossils from the Atlas Mts show that Springboks (of the living genus, *Antidorcas*) were already adapted to cool Eurasian-type habitats some 4 mya. Today's Springboks survive in SW Africa, the main region of the continent that has remained both dry and (periodically) cool. This region has been connected with N and NE Africa by arid corridors during every major Ice Age.
FOOD Broadly a summer grazer and winter browser, the Springbok can survive on the residual moisture in plants. In the absence of any surface water it seeks out succulents, cucurbits and even paws out shallow roots. It feeds most intensively around dawn and dusk. The staple in some areas consists of nine species of grasses and 11 species of shrubs but it has varied tastes. Some of the grasses favoured are coarse- or hard-stemmed species, such as bristle grass (*Aristida*), love grass (*Eragrostis*), stargrass (*Cynodon*), buffalo grass (*Panicum*) and rush grass (*Sporobolus*).
ADAPTATIONS Several adaptive traits distinguish this antelope and its numerous fossil antecedents. One of the most important is modification of the teeth for coping with coarse plants on dry winter pastures. Springbok teeth are more like those of a coarse-grass grazer than the narrower teeth

of herb- and leaf-eating gazelles. A more abundant food supply permits bigger, denser herds to form and more competition among Springbok males during the rut. Another is accommodation to permanent, large herds (as opposed to scattered groups on territories) involving increased competition, expressed in more frequent and severe head-butting. Severe buffetings of the head favoured the development of hollow, backward-swept horns which are better able to absorb the force of heavy blows and so better insulate the brain.



Springbok, male (*left*) and female (*right*)

BEHAVIOUR Females are highly mobile, moving quite independently of one another (but with current offspring). Because they form no close attachment to others or to territory, less is known of them than males, which comprise three main classes: immatures; unattached, non-breeding 'bachelors'; and territorial, breeding males. Breeding males normally ignore subordinate 'bachelors' but periodically enter a rut in which they become fiercely intolerant of all other males and seek to detain passing females within their 25–70ha territory. The rut can occur at any time and lasts 5–21 days; females that are not already pregnant may come into oestrus within a day or so of the male's rut. Large numbers of young are therefore born about 6 months later in a synchronised but unpredictable birth peak. However, births tend to peak in summer within the summer rainfall area of the Cape. Newborns lie up for a few days and run with their mother's group within 3 or 4 weeks. Females are sexually mature at 7 months but males are seldom sexually active until they have full-sized horns and have won a territory. They are known to live for at least 10 years (probably a lot more).

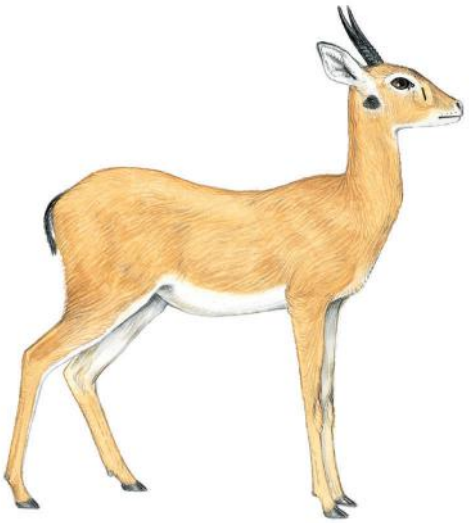
ADAPTATIONS The name 'Springbok' comes from the mainly juvenile and subadult habit of leaping up in a series of 'pronks', or hunch-backed bounces, that appear somewhat haphazard or playful at a superficial glance. In fact the pronking animal is extremely alert and watchful as it circles round or casts about from left to right. By slowing down the speed while maximising the height of its jump the young animal can take a series of bearings, not only on its physical surroundings but also on the position of predators and other Springboks. It was formerly assumed that pronking was a warning or, more recently, a 'flaunting of fitness' in the face of disturbance by humans or other predators. Both explanations could be incidental benefits but a primary function of pronking is learning orientation in inexperienced animals; adults seldom pronk, presumably because they already know their surroundings and neighbours.

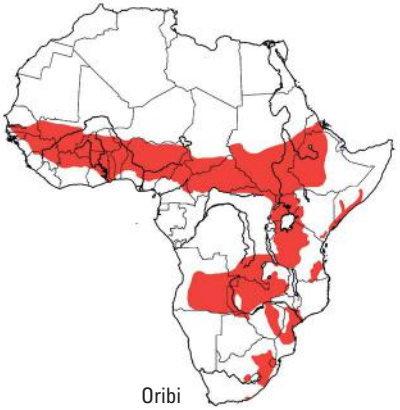
There is also a social dimension to pronking. The white hairs that flare up into view with each jump are saturated with scent from the glands that line the spinal pouch or marsupium. As a result, jumps broadcast both visual and olfactory messages to other Springboks. A static version of the pronk suggests a meaning for the message and a possible precursor for the evolution of both pouch and pronk. Young animals appease threatening adults by lowering their heads and presenting their rear ends for an olfactory inspection. 'Presenting' during a soaring and eye-catching jump may represent a fast and efficient way of broadcasting an appeasing message. All ages and sexes tend to pronk more frequently immediately after rain, when evaporation and drying-out fills the air with strong soil and plant scents that superimpose upon those of the buck. The release of dorsal scent by all or most members of a group superimposes the Springbok's signature on its surroundings. The scent may be both generally attractive to all Springboks, as well as containing specific indications about the status of an individual. If this social ritual is combined with scanning and memorising the landscape and its signposts, pronking evidently contributes to survival in at least two important ways. Just how well the Springbok remembers geography is revealed by its phenomenal capacity to 'home' back to small territories after months of travelling. Its return journey can begin at a moment's notice when the rains return.

STATUS Most Springboks in South Africa are now effectively a form of livestock that lives on fenced farmland. In parts of Namibia and in the Kalahari nomadic movements continue but are increasingly constrained by steady expansion of the livestock industry.

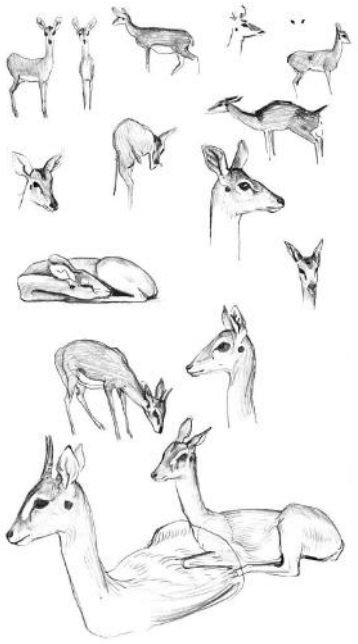
ORIBI Ourebini

Formerly included in Neotragini, Oribi is a highly distinctive form of antelope with some distant and still to be studied relationships with the Reduncini.





Oribi



ORIBI *Ourebia ourebi*

OTHER NAMES Fr. *Ourébi*. Ger. *Bleichbockchen*. Swah. *Taya*.

MEASUREMENTS HB 920–1,400mm. T 60–150mm. Sh. ht 500–670mm. W 12–22kg (♀ ave. 2kg heavier).

RECOGNITION A tall, slender antelope of medium-small size and sandy body colour (yellowish or reddish tinted), with white undersides, upper throat, mouth and ear linings. The light-coloured muzzle deflects down sharply from the forehead (unlike the black-bridged retroussé nose of the Steenbok; nor are the eyes rimmed by intensely black lids as in the Steenbok). The ears are of moderate size. In addition to hoof (pedal) and groin (inguinal) glands, the Oribi has scent brushes below the knees and ankles and black gland patches below the ears. The face glands (preorbital) are also exceptionally well developed. Alert and shy, the Oribi's piercing whistle is frequently heard as it flees from the observer with a characteristic rocking-horse gait.

GEOGRAPHIC VARIATION *O. o. ourebi* (S and SE Africa), *O. o. hastata* (SE Africa between R. Ruaha and R. Zambezi/R. Shire), *O. o. cottoni* (upland E Africa), *O. o. montana* (NE Africa east of the R. Nile), *O. o. haggardi* (coastal Kenya and Somalia), *O. o. goslingi* (northern savannas, R. Chari/R. Nile), *O. o. quadriscopa* (Senegal to Chari, savannas).

DISTRIBUTION Mainly Sudanic, E and SE Africa on fire-climax grasslands but under relatively reliable rainfall regimes.

HABITAT Grasslands maintained by fire or heavy grazing. They prefer flats or gentle slopes and are commonest on open lawns of grass kept short by compaction, termites, poor soils, fast drainage,

trampling or heavy grazing by large herbivores. Such herds not only improve the Oribis' range, but may also buffer them from predation; Oribis tend to decline wherever such herds have been severely reduced or exterminated. On extensive floodplains Oribis favour the less waterlogged areas where termitaries, herbs and woody growth provide cover and supplement the diet. In exceptional habitats densities of 45 per km^2 have been recorded.

FOOD Mainly fresh green grass typical of fire-climax communities, i.e. *Themeda*, *Hyparrhenia*, *Loudetia* and *Eulalia*. However, many other grasses are taken, as well as various grassland herbs and the foliage of several shrub and tree species. Oribis cluster on scarce, short lawns within the sea of rainy-season long grass. Movements out of territories are typically oriented towards favourite mineral licks, which are visited regularly.

BEHAVIOUR Females are larger than males and are independent in their movements but, by becoming the object of continuous attention from a single male, each adult female determines the area within which he is intolerant of other males. This area becomes a shared territory in which each partner repels others of the same sex (but females tolerate adult female offspring). Pairings last for many years. Such territories adjoin supplementary pastures, refuges or salt-licks where other families may gather. Each territory is traversed daily by the male, who exchanges scents with females and their young during elaborate, shared 'dung ceremonies'. Throughout the day he assiduously marks plants and soil with his own excreta and secretions.

Seasons, predators and reproduction all influence activity. Thus Oribis rest longer on hot afternoons and may lie up during heavy rain. In exposed areas they prefer to graze at night, notably during full moons during the dry season. Their whistle may serve as both alarm and also to advertise shifting positions and movement. More breathy, puffing whistles keep neighbours informed. They bleat if pursued or captured. There is a mating peak in southern Africa during April with births 7 months later. The precocious young is adept at concealment for 3–4 days. Thereafter it begins to follow the mother but still seeks shelter from time to time. Growth is very rapid and near adult height is reached, with weaning, by about 4 months. Females are fertile at 14 months. A preponderance of males develops in some areas and territories may be dominated by older, even aged males. Animals are known to live for up to 14 years.

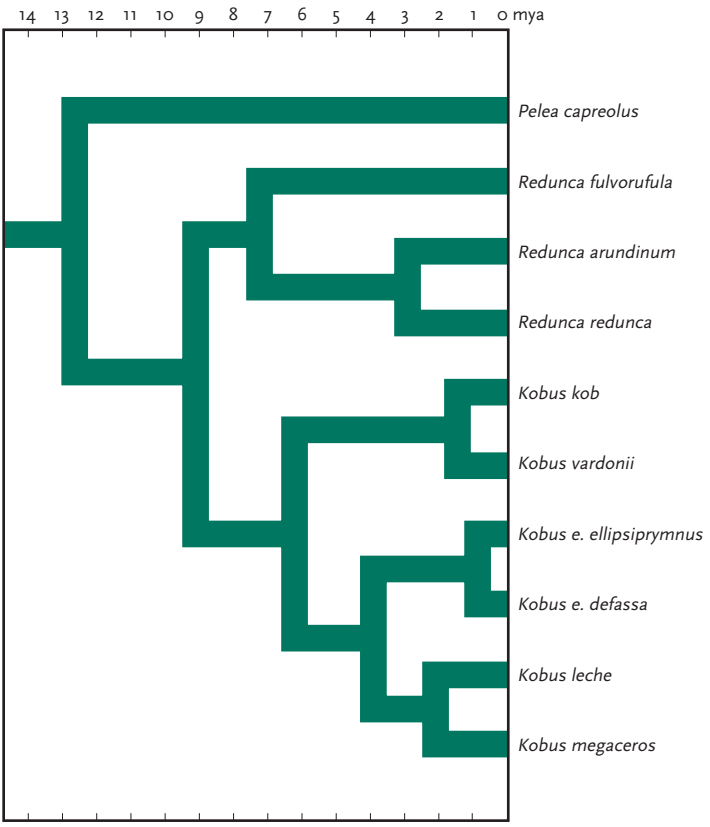
ADAPTATIONS Female Oribis are thought to excrete attractants that provoke continuous interest in males. Male alertness to female excretory posture, urine and dung is relentless and stimulates him into non-stop glandular marking. On an adult male, there are 14 sites secreting odours and all likely to contribute to saturating the core of his territory with his individual scent signature. Techniques for marking out small male territories within dense thicket were evolved by ancestral dwarf antelopes. Their modification for use in much larger territories in open grassland has involved the specialisation of male Oribis into full-time factories and dispensers of odours. It is known that these odours are not only charged with information about their producers but have the potential of strongly influencing the behaviour of those smelling them. Because all inhabitants of a territory mix and exchange scents at daily 'dung ceremonies', dangerous, costly confrontations are avoided through repetitive habituation. More important, a female is so frequently assailed with reminders of her partner's particular signature that she becomes habituated to his particular scent signature as an essential attribute of her environment. The male gains an important reproductive advantage in that the female stays within an area that he can control without physical coercion.

STATUS Residential habits may make Oribis poor colonists and this may influence the very patchy distribution of at least seven subspecies. Elimination from many localities has taken place this century. Nonetheless, the species is still widespread and not endangered overall.

REDUNCINES, KOBS Reduncini

Rhebok	*Pelea capreolus*
Reedbucks	*Redunca* (3 species)
Kobs	*Kobus* (5 species)

RECOGNITION Medium-sized to large antelopes with slender to stocky legs, a long, well-muscled body and a relatively thick neck (especially in males). The largest species are shaggy; smaller ones are sleek or slightly fleecy. Most are tawny or tan but males of the larger species can be dark brown or even black (usually with white or off-white markings). Horns, on males only, are

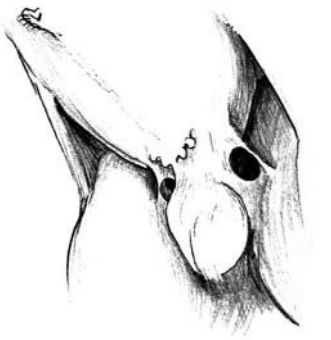


Tentative phylogenetic tree for Reduncini (modified from Hernández Fernández & Vrba 2005).

annulated and always curl forward at the tip (this corresponds with forward striking with the head, powered by muscles that help shape the bulging neck). Both preorbital and pedal glands are vestigial or absent but all have well-developed inguinal glands in the groin. All have a pungent overall odour that emanates from sebaceous glands and films the entire body. This provides a seal against water loss and possibly some insulation against temperature extremes but is also likely to carry socio-sexual signals (as must their musky urine). Reedbucks have black, glandular patches below the ears, which, among other messages, advertise the female's breeding condition. The smaller reduncine species make ritualised 'rocking-horse' displays that apparently signify subordination. These may be the long-grass equivalent of the 'stotting' or 'pronking' of antelopes in more open habitats.

The enigmatic Rhebok is a uniquely South African species. Its scientific name, *Pelea*, latinises its Tswana name, *phele*, while *capreolus* means 'goat-like' or 'sheep-like', a reference to its chunky, mountaineering hooves and short, crinkled wool.

GENEALOGY Reduncines probably began to evolve from neotragine grazers about 14 mya. The earliest fossils, about 11 million years old, come from East Africa but reduncines were present in India by 5 million years ago. Earlier names betrayed much uncertainty about the Rhebok's affinities. The archaic and obsolete *Cemas*



Reduncine inguinal glands (in male Reedbuck).

embraced such diverse antelopes as Klipspringers, Oribis, Springboks and reedbucks. *Redunca villosa* and *Eleotragus villosus* (both meaning 'hairy reedbuck') put it firmly in the kob tribe while *Antilope lanata*, 'woolly antelope', was suitably generalised and descriptive. Sustained adaptation to a unique herbivorous niche in the temperate mountains of southern Africa has resulted in some convergence with sheep and disguised hints of likely common origins with Oribis and the kob tribe.

GEOGRAPHY Now restricted to well-watered areas of Africa, the reduncines' dispersal to India and North Africa implies long periods of moist conditions along the Nile valley, other rivers and along coastal forest zones. This is because they are poor dispersers, keeping a close attachment to their natal area.

ECOLOGY Sumplands are rich in food but are unstable because they dry out or catch fire. Antelopes find it difficult to cope with their fluctuating water levels, sticky soils and rapid growth of impenetrable grasses. Only lechwes, with swamp-adapted hooves, can reside permanently in wetlands. For the rest, accommodation to radical seasonal changes inhibits extreme specialisation, making the kob tribe unusually homogeneous. The smaller Mountain Reedbucks are the most conservative but are secondarily adapted to coarse grazing and cool climates in upland pastures.

The instability of their enormously productive habitats encourages substantial fluctuations in numbers. This is exacerbated by a weak ability to disperse. Seasonal changes lead to short-distance movements that also cause crowding, sometimes of spectacular proportions (notably in Kob).

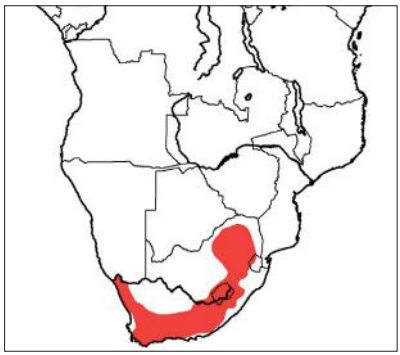
NATURAL HISTORY To accommodate both crowding and dispersal, reduncines have very flexible relationships between the sexes. Females are usually independent and, while in oestrus, are the object of intense competition between males. Big differences in the size, morphology and behaviour of the sexes correspond to separate male and female strategies. The females of reduncine species have more in common than the males (which look and behave very differently from species to species).

Study of their social systems, which are largely mediated by invisible scent cues, have scarcely begun. However, it appears that fundamentally different social systems correspond with the particular kind of refuge sought by each species. Because reduncines lack stamina an animal facing danger has three possible sources of refuge: (a) thick cover (reedbucks, Waterbuck); (b) water (most species, but especially lechwes); (c) dense herds (Kobs). All species appear to track each other like bloodhounds and clearly broadcast much information through glandular scents.

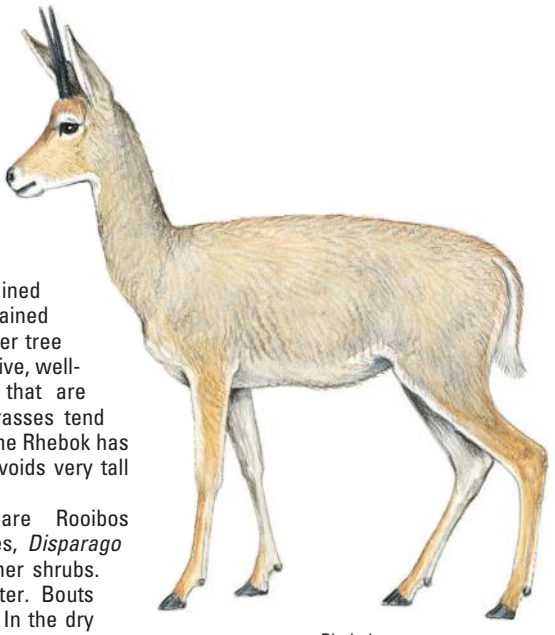
ADAPTATIONS Because they are the major bovid lineage adapted to valley grasslands, reduncines have considerable potential for rational exploitation, having the fastest growth rates of any bovid, insignificant disease problems and very acceptable meat and hides. Large populations of the more social species are unlikely to survive unless their potential for scientifically monitored sustained-yield cropping is realised because they occupy habitats with a high priority for agriculture or for inferior forms of livestock development.

RHEBOK *Pelea capreolus*

OTHER NAMES Grey Rhebok, Vaal Rhebok.
Fr. *Rhebuk, Péléa*. Ger. *Rehantilope*.
MEASUREMENTS HB 1.05–1.25m. T 100–200mm.
Sh. ht 700–800mm. W 18–30kg.
RECOGNITION A long-legged, long-necked antelope with a woolly, tawny-grey coat rounding the body contours. The long, narrow muzzle ends with a small mouth below a blunt, swollen nose. The ears are very long and pointed, the forehead swollen and the black-lidded eyes are very prominent in a white surround. The tail is bushy and white below. Undersides are pale. The males have very vertical spike horns that can be as long as 290mm. During ritualised postures, with erect neck and tucked-in chin, the unusually short back of the head becomes noticeable.



Rhebok



Rhebok

DISTRIBUTION Mainly in upland South Africa but actually descends onto sand dunes in the Cape. Most numerous in strongly seasonal pastures above 1,000m, staying on the heights during the rains but descending to lower slopes when dry.

HABITAT Highveld, 'sourvelt' and secondary grasslands, mainly on plateaus and mountains. While some of its pastures are maintained by fire, most are on dry, deeply drained slopes where very severe frosts deter tree growth. These are patchy but extensive, well-established and ancient pastures that are peculiar to southern Africa. The grasses tend not to grow very tall or rank so that the Rhebok has a clear view. Unlike reedbucks, it avoids very tall grass.

FOOD Preferred browse plants are Rooibos (*Aspalathus linearis*) and the daisies, *Disparago* and *Metalasia*, as well as many other shrubs. The Rhebok is independent of water. Bouts of grazing and resting are irregular. In the dry season it tends to browse for longer (and at night) in valley bottoms. While the weather is hot it rests up during the heat of the day.

BEHAVIOUR Harems comprising a single male and up to five females and their offspring provide a basic social unit that can proliferate into a small herd (maximum 14). These live on stable home-ranges of 15–135 ha (smaller and higher in summer, larger and lower in winter). The harem male spends much time patrolling and marking out their home area with urine (loaded with extra scents and melanin pigment from a preputial gland that is unique to the Rhebok). He regularly surveys and postures from the top of mounds or ridges, or near rocks and trees where he also excretes (but not on a midden). If in sight of another male he stamps, makes a sharp, clacking call and prances with various bouncy, rocking-horse gaits. Rhebok are very vocal with a repertoire of whistling barks, bleats, hisses and snorts. Confrontations between males are frequent along boundaries but charges nearly always stop about 1m apart, with heads down and horns lunging and stabbing without actual contact. Territorial defence and 'air-cushion fighting' are commonest during the summer mating season (January–April). After a 7-month gestation one, occasionally two, young are born in a secluded place. The young remain concealed for 6 weeks before joining the mother and her group. Yearling males are evicted from harems. From about two years of age such males seek to take up territories of their own. Short visits from females still in their parental groups gradually get prolonged until they become permanent residents of the new territory. Male scent and male behaviour appear to be actively attractive to female Rheboks and there are few signs of them being coerced by males.

ADAPTATIONS Although it has been suggested that the Rhebok could share a common ancestry with sheep, their similarities are certainly convergent. Cold South African winters on dry, stony uplands are miniature copies of environments in the mountain chains of Eurasia where sheep evolved. Rhebok flee uphill, seeking exposed heights where they can monitor any disturbance below.

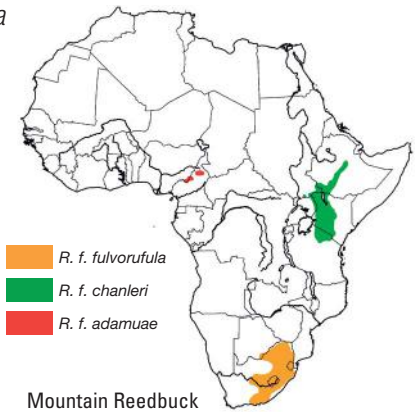
STATUS The Rhebok is well represented in numerous reserves, national parks and private farms where it is, for the most part, compatible with livestock. Although it has been exterminated over a large part of its former range, which is now very fragmented, it is common within these fragments. Not endangered but very susceptible to depredation by dogs.

REEDBUCKS *Redunca*

Mountain Reedbuck *Redunca fulvorufula*
Bohor Reedbuck *Redunca redunca*
Southern Reedbuck *Redunca arundinum*

MOUNTAIN REEDBUCK *Redunca fulvorufula*

OTHER NAMES Fr. *Redunca de montagne*. Ger. *Bergriedbock*. Swah. *Tohe ya milima*.
MEASUREMENTS HB 1.10–1.36m. T 170–260mm. Sh. ht 600–800mm. W 19–35kg (♀), 22–38kg (♂).
RECOGNITION A moderately-sized antelope with slender legs and a chunky body. The soft, fleecy fur is tawny grey, with white underparts and a bushy white underside to the tail. It is the smallest of the reedbucks and its eyes and their sockets are peculiarly prominent, as is the black gland-patch below the ear and, in males, the short, forward-curved black horns.
GEOGRAPHIC VARIATION *R. f. fulvorufula* (South Africa), *R. f. chanleri* (E and NE Africa), *R. f. adamuae* (N Cameroon).

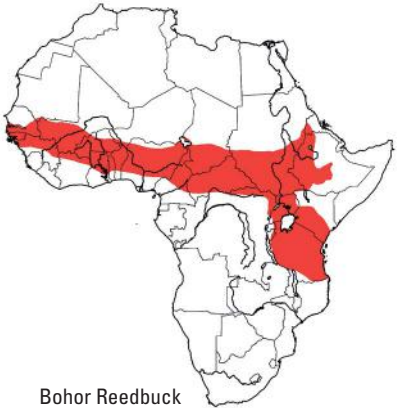


Mountain Reedbuck

DISTRIBUTION Widely separated mountains in S and NE Africa, with an outlying relict population on Mt Adamua in the Cameroon uplands. They live in cool, rather dry, mountainous regions mostly above 1,500m and up to 5,000m. These may be the vestiges of its range during more favourable glacial periods.
HABITAT They prefer grassy ridges in broken rocky country, on small outcrops and volcanic lava flows and cinder cones. In Kenya, Mountain Reedbucks prefer the scrub-grass ecotone between slopes covered in camphor (*Tarchonanthus*) and open grassy valleys. They are often less nocturnal than other reedbucks.
FOOD Almost wholly grazers, with *Themeda*, *Hyparrhenia* and *Cymbopogon* recorded as favourite food plants. Mountain Reedbucks can live for a while without water but lose condition rapidly. Fluctuating food leads to fluctuating numbers.

BEHAVIOUR Females with young form parties of two to eight but temporary aggregations of up to 50 can form. Female home-ranges in southern Africa are 36–76ha but male territories average 28ha. Female ranges are unusual, therefore, in overlapping those of several males that do not control their movements. Ranges cover a sample of the available habitats and run from hilltop to valley. 'Bachelor' groups are temporary and tenuous in where they can live and high mortality among males tends to skew sex ratios. A single young is born after an 8-month gestation. It remains well hidden for up to 3 months before joining its mother's group. Prolonged hiding may reflect special risks from eagles, large cats, jackals and baboons in their habitat.
ADAPTATIONS Intimate knowledge of their home-ranges allows them to mitigate predation while the ubiquity of grass seldom makes them limited by food. However, strictly sedentary habits inhibit dispersal and render isolated populations vulnerable to extermination during prolonged droughts or after sustained over-hunting.

BOHOR REEDBUCK *Redunca redunca*


Bohor Reedbuck

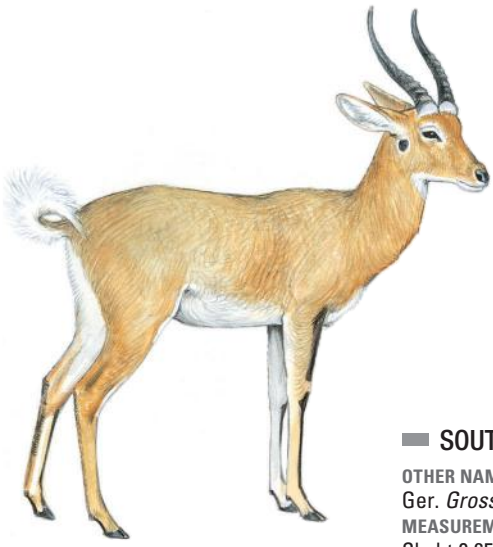
OTHER NAMES Common Reedbuck. Fr. *Redunca*. Ger. *Gemeiner Riedbock*. Swah. *Forhi, Tohe*.
MEASUREMENTS HB 1.00–1.35m. T 180–200mm. Sh. ht 650–890mm. W 35–45kg (♀), 43–65kg (♂).
RECOGNITION A medium-sized, sandy-coloured antelope in which the slender proportions of females contrast markedly with the thick-necked, hook-horned males. It has deeply pocketed glands in the groin, black patches below the ears and is oily or greasy all over from sebaceous ducts at the roots of all hairs. Its loud whistles (mainly uttered at night) are the surest guide to its presence, especially in tall, wet-season grasslands, where it is seldom seen. The size of horns appears to correspond to some extent with densities, i.e. stubby horns in East Africa at dispersed, lower densities and longer, splayed horns in the Nile valley with seasonally concentrated, high densities.
GEOGRAPHIC VARIATION *R. r. redunca* (northern savannas), *R. r. cottoni* (Sudd region), *R. r. bohor* (Ethiopia), *R. r. wardi* (East Africa).
DISTRIBUTION From Senegal to Ethiopia, south to L. Tanganyika and the Rovuma valley. Particularly wide shallow floodplains associated with major lake and river systems, i.e. R. Niger, R. Nile, R. Rufiji, L. Chad and L. Victoria.
HABITAT Mostly large-scale sump grasslands that are highly unstable, with extensive annual flooding, drought and fires. They are peculiarly well adapted to cope with these extremes and to changes in height and quality of the food supply and shelter grass. While they are dispersed, densities of about five animals per linear kilometre of valley bottom are common. During periods of concentration, densities of more than 100 per km^2 have been observed and they are not uncommonly found at distances of 25km from water during droughts on open floodplains.
FOOD Exclusively grazers, with a recorded preference for typically dominant species, i.e. *Hyparrhenia*, *Sporobolus*, *Heteropogon* and *Themeda*. Feeding mainly after dark, Bohor Reedbucks may make nightly forays to graze up to 8km from their day-time refuge. As the quality of the grazing declines during the dry season, nocturnal feeding alone becomes insufficient. Eventually some animals may keep grazing both day and night.
BEHAVIOUR Females disperse into discrete home-ranges during the wet season (when most young are born). Males also appear to be very scattered at this time (in the absence of females they can be quite tolerant of each other). Fires and drought (beginning in about October in the northern savannas) drive the animals into larger groupings. By the early dry season males are intensely intolerant of each other and it is probably repeated fights and stand-offs with neighbours that define, perhaps temporarily, their 'territories'. In rare situations where home-ranges are stable, 'territories' may be an appropriate term but their typically unstable habitat favours a system in which females search out the best and safest remaining pastures while males fight for mating rights over each female or group of females.

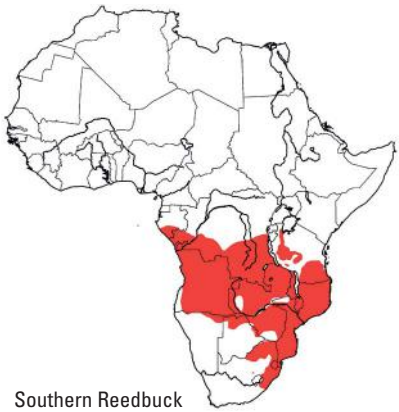
The glandular ear patch is thought to play a part in advertising oestrus. In courtship males circle females making a bleat like a toy trumpet. After a gestation

of 7 months one young is born and it remains well hidden (but with daily changes of retreat) for at least 2 months. Young males sometimes form 'bachelor' groups before becoming fully mature at about 4 years. Females are fertile by 1 year. Animals live for at least 10 years.

ADAPTATIONS Whistling and ritualised bounding are two conspicuous features of Bohor Reedbuck behaviour. Both are effective forms of communication in their dense, obstructed habitat. Leaps differ in amplitude, length and style. Likewise, whistles vary in number of blasts and in pitch. In the dry season choruses of whistling can be heard whenever animals change their positions, especially at night as they emerge to graze.

STATUS Very common and widely distributed. This reedbuck continues to survive even in the face of agricultural expansion.





Southern Reedbuck

SOUTHERN REEDBUCK *Redunca arundinum*

OTHER NAMES Fr. *Cobe des roseaux, Eléotrague*. Ger. *Grossriedbock*. Swah. *Tohe ya kusini*.

MEASUREMENTS HB 1.2–1.6mm. T 180–300mm. Sh. ht 0.65–1.05m. W 50–85kg (♀), 60–95kg (♂).

RECOGNITION The largest reedbuck, with a fine, almost woolly coat. Some are light buff, some dark brown, others are in between. The underside is paler, as is the chin and throat. Black-and-white markings on the front of the forelegs are prominent. The horns, only on males, grow up to 450mm long and resemble a diminished version of the Waterbuck's, with a pale base. The tail is large and bushy, with white on the underside.

GEOGRAPHIC VARIATION *R. a. arundinum* (south of the Zambezi), *R. a. occidentalis* (tropical Africa).

DISTRIBUTION SE and central Africa, with a substantial overlap in range with the Bohor Reedbuck in Tanzania (where it is rare).

HABITAT Widely distributed in the rank grass valleys and glades within miombo (*Brachystegia*) woodlands where the greater part of their range is contained. Best adapted to mosaics of scrub and grass. They decline if denser, taller thicket replaces more open country but flourish in tall grass patches on the margins of more waterlogged swamps.

FOOD Favourites are dominants in their habitat, i.e. *Hyparrhenia*, *Panicum* and *Leersia*, but Southern Reedbucks are not selective or specialised grazers. Much feeding is nocturnal and they are dependent on water.

BEHAVIOUR Converging on water sources in the dry season, they only disperse widely when it is wet and the grass grows tall again. Home-ranges get compressed to 5–35ha during the dry season but expand greatly during the rains. Births peak in the rains and both mothers and their young tend to remain well concealed in the long grass. As water gets scarcer and the fires begin female attachment to males becomes more obvious and frequent. Each male actively keeps other males away from one female (more if he is able). Contact is maintained by means of whistles and leaping displays but it is thought that scent trails through the grass provide the main clue to each animal's whereabouts.

One young is born after a 31-week gestation. Female young are unusual in being the first to leave their mother, as they become fertile at about 1 year. Males may remain with their mothers into their third year, by which time their horns are conspicuous and frequent appeasement of their mothers' 'consort' may be necessary.

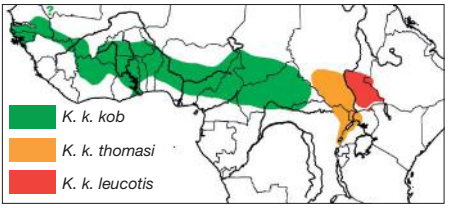
ADAPTATIONS Both females and young males make 'rocking-horse' displays towards adult males. Running around at speed they throw up their rumps and white tails in long, floating bounds. A popping sound is often made with the leaps, just as the hindlegs jerk back and out at the peak of each leap. The noise appears to result from a release of scented air from the inguinal pockets situated in each groin. Whistles are also commonly uttered with these jumps and the whole sequence would seem designed to appease the adult males.

STATUS Although their total range is now very fragmented, Southern Reedbucks are well represented in reserves and parks. Not endangered.

KOBS *Kobus*

Kob	*Kobus kob*
Puku	*Kobus vardoni*
Southern Lechwe	*Kobus leche*
Nile Lechwe	*Kobus megaceros*
Waterbuck	*Kobus ellipsiprymnus*

KOB *Kobus kob*



Kob

OTHER NAMES Fr. *Cobe de Buffon*. Ger. *Grasantilope*. Swah. *Mraye*.

MEASUREMENTS HB 1.6–1.8mm. T 100–150mm. Sh. ht 0.82–0.92m (♀) 0.9–1.0m (♂). W 60–77kg (♀), 85–121kg (♂).

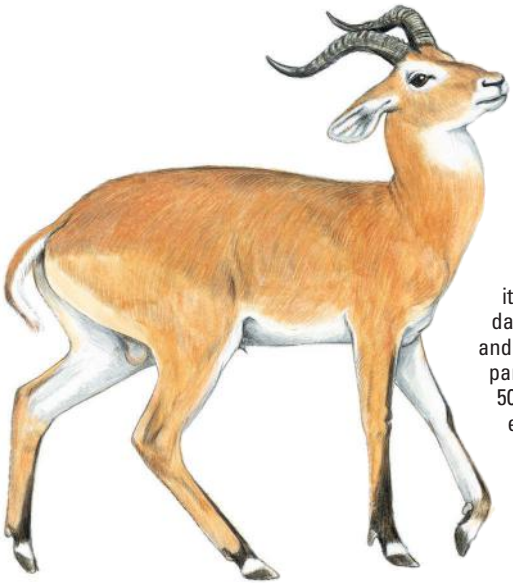
RECOGNITION A medium-sized antelope with a muscular, deep, rounded body and neck (especially in males) and robust limbs. The males have thick, lyrate horns. Females are various shades of reddish or yellowish ochre, with a white underside and markings on the face, ears and hocks. Male colouring varies from rich cinnamon rufous, or pale yellowish brown, to black and white in the Sudd floodplain. Piebald colouring corresponds with fewer predators. Dark markings or tints occur on Kobs from other large flood-plains and around the Sudd margins, blurring the boundaries between forms.

GEOGRAPHIC VARIATION Western Kob, *K. k. kob* (northern savannas); Uganda Kob, *K. k. thomasi* (East Africa and NE DR Congo); White-eared Kob, *K. k. leucotis* (Sudd floodplain).

DISTRIBUTION Senegal to W Ethiopia to L. Victoria littoral.

HABITAT Low-lying flats or gently rolling country close to permanent water, without seasonal extremes. They favour short swards, cropped and trampled by concentrations of large ungulates or fire-induced grasslands. Where numerous enough, they keep down limited areas of sward ('kob fields') through the sheer weight of their own numbers. Totally dependent on regular drinking, Kobs remain tied to areas within a short walk of water. They retain strong attachments to both grazing grounds and watering points, returning day after day and season after season.

White-eared Kob *K. k. leucotis*, male head



Uganda Kob *K. k. thomasi*

FOOD Grazers of the commonest grasses, notably *Hyparrhenia*, *Brachiaria*, *Setaria* and *Paspalum* species, among many others. Seasonal changes in diet (i.e. *Cenchrus* in the rains) emphasise the Kobs' preference for a short sward.

BEHAVIOUR Kob populations are prone to great fluctuations in numbers but these get compressed because attachment to locality and routine inhibits dispersal. Resident populations move daily between habitual grazing grounds and watering places. These grounds are parcelled out into male territories of up to 50ha. The female strategy of going to water en masse leads to female aggregations that increase the stimulus that they present to males. The males respond with more competition and fighting among themselves. Mating appears somewhat chaotic and would be more so without lengthy pauses at specific spots along the route from the grazing grounds to drinking places. Sexually active males scramble for matings in these heavily contested 'assembly fields' where up to 40 males may cluster in an area of about 1ha. Triangular territories radiate out from one or more 'hubs' within such areas, each 'hub' being signposted by a steady accumulation of dung and urine-soaked soil. Recent research has shown that the primary attractant that draws sexually active adults of both sexes to these heavily scented 'hot-spots' is the oestrogen-charged urine of oestrous females. Under the influence of the pervasive musk wafting from such centres, receptive females allow themselves to be mounted by one or more of the associated territorial males. The considerable expenditure of energy required to defend their minuscule patches in the 'assembly fields' ensures that males are quickly exhausted. Tenancies may only last a few hours, so males are almost as transitory as females. By contrast, territories on the grazing grounds may last a year or more.

Stereotyped, small-scale movements of a few kilometres are typical of populations resident in enclosed valley systems. Where the sump area is larger, as in the Sudd, Kobs become migratory but their movement over many hundreds of kilometres is equally bound by tradition. Here too, mass movement induces the formation of territorial 'slices' of ground arranged around beacons of female urine. These radial slices of territory are fiercely contested by males.

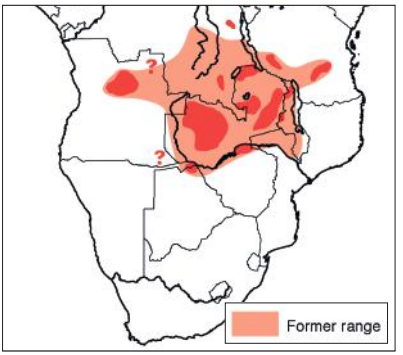
In South Sudan virtually all females give birth along the south-eastern borders of the Sudd basin towards the end of the rains (September–December). After migrating 200km or more north, mating takes place along the eastern rim of the basin at a time when the plains are at their driest. After an 8-month gestation one young is born. Like reedbucks, their first 6 weeks are spent in hiding, after which they join their mothers and other Kobs on the grazing grounds. Females are fertile at one year, males become sexually active at 3 years.

ADAPTATIONS If Kobs evolved from a type of reedbuck their major innovation is the ability to congregate. Unlike some semi-social antelopes (such as Oribis) they do not scatter when chased or attacked but often move as a single mass. This inhibits smaller predators while their open habitat protects them from some larger ones (Lions are temporary, nomadic visitors to floodplains).

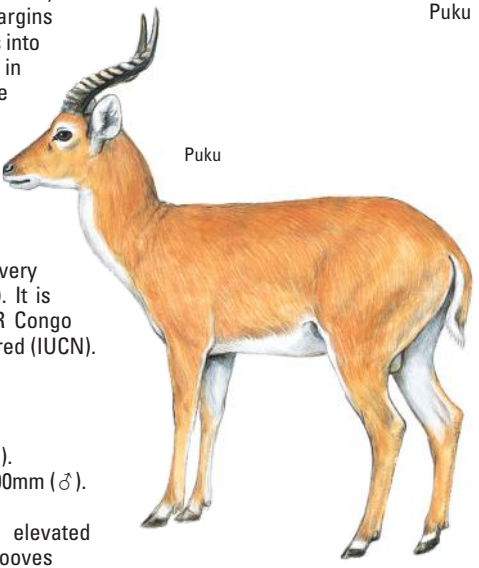
STATUS In spite of having been eliminated from many areas (notably from all the shores of L. Victoria), Kobs readily recover from near extermination. In terms of energetics, they assimilate poor-quality food, convert it to meat and grow faster than any other bovid. Kobs are potentially an exceptionally valuable resource. Fortunately they are still widely distributed and are not endangered, but a blinkered, primitive livestock industry still fails to appreciate the value of indigenous African ecosystems and species.

PUKU *Kobus vardoni*

OTHER NAMES Fr. *Puku*. Ger. *Puku*. Swah. *Puku*.
MEASUREMENTS HB 1.26–1.42m. T 280–320mm. Sh. ht 770–830mm. W 48–78kg (♀), 67–91kg (♂).
RECOGNITION This southern relative of the Kob is sometimes treated as a mere subspecies. It has heavier proportions (particularly noticeable in the female), a coarser coat and shorter, less lyrate horns with less 'stem' than the Kob.
HABITAT Upper basins of the R. Zambezi, Congo R. and R. Rufigi. It inhabits the margins of lakes, swamps, rivers and floodplains and is more tolerant of narrow grasslands and park-like woodlands than the Kob. It lives on higher ground in the rainy season, descending in the dry season to graze the margins of lakes and rivers. It sometimes amalgamates into parties of 50 or more in the dry season (3–15 in the rains). Territories are spaced out and there is year-round breeding.
FOOD Preferred grasses are *Brachiaria* (especially January–March), *Eragrostis* (July–August) and *Vossia* shoots (December). The Puku will feed off lawns.
STATUS Exterminated from several parts of its range, the Puku is locally endangered or very rare (Tanzania, Botswana, Namibia, Malawi). It is still common and widespread in parts of DR Congo and Zambia, where it is listed as not endangered (IUCN).

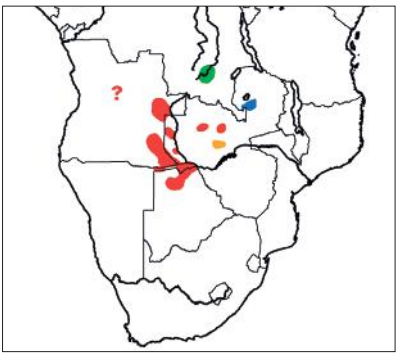


Puku

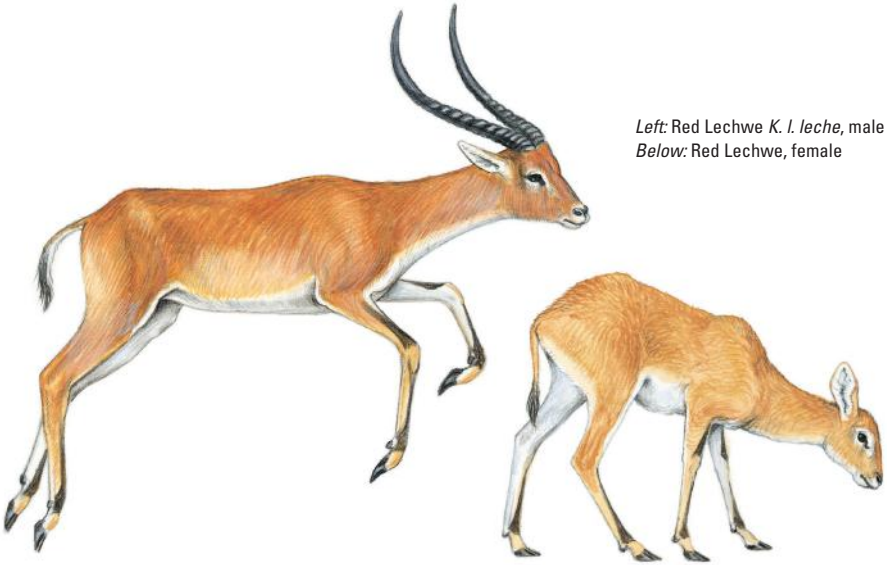

Puku

SOUTHERN LECHWE *Kobus leche*

OTHER NAMES Fr. *Cobe lechwe*. Ger. *Litschi*.
MEASUREMENTS HB 1.3–1.7m (♀), 1.6–1.8m (♂). T 300–450mm. Sh. ht 850–950mm (♀), 850–1,100mm (♂). W 60–95kg (♀), 85–130kg (♂).
RECOGNITION A heavily built antelope with elevated haunches, notable for its splayed, elongated hooves (generally hidden from view in water, mud or grass). It has large, widely spaced eyes, a rather short muzzle and, in males, long, slender but heavily annulated horns that sweep back (500–920mm). Females are red to tawny, graduating to white on the underside and throat, with white borders around the eyes and muzzle. Male Red Lechwe have similar colouring but black fronts to the white legs extend up onto the body in other subspecies. Here they spread with age. In one population, the Black Lechwe, this spread continues until fully mature males are boldly black and white. Normally phlegmatic, they rush through the shallows when disturbed, with clumsy, galloping bounds which sometimes begin with what David Livingstone described as a 'waddling trot'.
GEOGRAPHIC VARIATION Red Lechwe, *K. l. leche* (NW Zambia, Angola, Botswana); Kafue Lechwe, *K. l. kafuensis* (Kafue flats); Katanga Lechwe *K. l. anselli* (DR Congo); Black Lechwe, *K. l. smithemani* (Bengweulu basin, R. Chambeshi).



Southern Lechwe



Left: Red Lechwe *K. l. leche*, male
Below: Red Lechwe, female

DISTRIBUTION Restricted to the flat, silted-up river basins of the central African plateau (mainly the headwaters of the R. Zambezi and southern Congo R. tributaries) where they occur only in permanently waterlogged areas, being totally dependent on water to drink and in which to find food and shelter.

HABITAT Along the unstable margins between swamps and shallow floodplains. The larger and flatter the basin, the larger are both the habitat and lechwe numbers. Females and their young tend to stay on the wetter end of this zone, adult males on the drier end. Keeping to the shallows/dry land margin involves continuous movement and distances of up to 80km may be travelled in very wet years (R. Chobe). Concentrations in favoured areas can reach temporary densities of 1,000 per km^2. In some areas herds may move inland to graze on short pastures following fires, moving mostly at night.

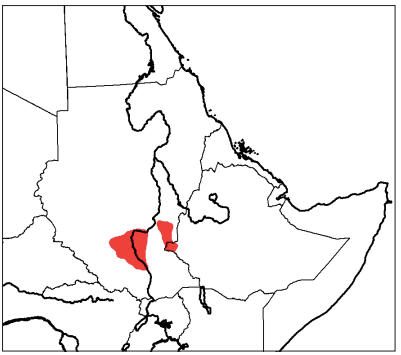
FOOD Favoured grasses are *Echinochloa*, *Panicum*, *Brachiaria*, *Paspalium*, *Acroceras* and *Oryza*; also the fresh shoots of trampled reeds (*Phragmites*). Most feeding takes place for a few hours before dawn and after dusk.

BEHAVIOUR Females seek out the best grazing, concentrating whenever it is localised, dispersing when it is widespread. They are unencumbered by any lasting bonds except with their young. The majority give birth during the late, hot dry season between July and October, but some breeding continues throughout the year. Males have a protracted rut during the early wet season (November–February) but sexual interest and the size of the testes decline throughout the late wet season and the dry season. All sexes tend to remain dispersed but sexually inactive males are forced into peripheral 'bachelor' herds that can become quite large (50 or more members). This pattern changes with the rising flood levels during the early rains.

Before the grasses have regrown, herds are at their densest and it is at this time that the rut begins. As females come into oestrous, and are presumably drawn by the scents of other sexually active animals of both sexes, they gather at 'hot-spots'. Access to these is fiercely contested by males, who crowd around them. Those closest to the hot-spots occupy the smallest areas and achieve the highest number of copulations but are quickly exhausted. Further from the centres, pressure is less continuous and intense. The males here exclude each other from larger areas more effectively and hold much longer tenancies (but they presumably inseminate fewer females). One young is born after a 225-day gestation. After lying up for some weeks the young emerge to join the female herds. Females are fertile by 18 months, males take more than 2 years and are not fully mature until 5 years. Animals live for up to 15 years.

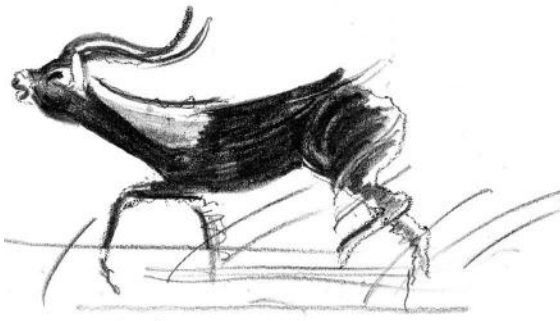
ADAPTATIONS Slow and clumsy on hard ground, lechwes are very strictly tied to swampy floodplains by their physiology and their soft hooves.
STATUS Southern Lechwes are known to have been exterminated in many peripheral areas, indeed one race (the Luena Lechwe, *K. l. robertsi*) has already become extinct this century. They are very poor colonisers and recolonisers. The separation and subsequent speciation of Southern and Nile Lechwes implies a much wider distribution in the past. Both the Kafue and Black Lechwes are well represented in national parks. Elsewhere they are being progressively displaced by cattle that are markedly less productive users of the habitat.

NILE LECHWE *Kobus megaceros*



Nile Lechwe

OTHER NAMES Mrs Gray's Lechwe. Fr. *Cobe de Mme. Gray*. Ger. *Weissnacken moorantilopen*. Dinka dialect *Abiok*.
MEASUREMENTS HB (est.) 1.3–1.7m (♀); (est.) 1.6–1.8m (♂). T 450–500mm. Sh. ht (est.) 0.80–0.85m (♀), (est.) 1.00–1.05m (♂). W (est.) 60–90kg (♀), (est.) 90–120kg (♂).
RECOGNITION A robust swamp antelope with longish hair, yellowish to russet in the hornless, smaller female. Like Southern Lechwe, it has a rather short face. The hooves are exceptionally elongated, the inner hoof much narrower than the outer. Males have double-curved, lyrate horns (500–870mm long) and their coats slowly darken over several years, changing from tawny russet to a pale reddish grey that darkens until it is a deep chocolate black. The underside, tail, back of the neck and upper shoulder are creamy white, as are the muzzle and surround of the eyes.
DISTRIBUTION The Sudd region of the White Nile close to the various tributaries that converge near Malakal. This is a single, spidery swamp system flowing over an alluvial plain with surface gradients as shallow as 70mm per km.
HABITAT Mainly confined to the river-flooded grasslands that lie between deep swamp (dominated by *Cyperus papyrus* and Sudd Grass, *Vossia cuspidata*) and the drier rain-flooded grasslands (dominated by thatch grass, *Hyparrhenia rufa*). This river-flooded zone, or toic, is dominated by Swamp Antelope Grass (*Echinochloa stagnina*), rice grass (*Leersia*) and wild rice (*Oryza*) and has numerous pools edged with bulrushes and water-lilies. Within the toic, Nile Lechwes follow the fluctuating margins between shallow floodwaters and drier ground. This involves continuous seasonal drifting up and down the flood tide lines. As floods deepen (about May) the animals move further from the river and/or upstream, travelling as far as 30–40km between their high- and low-flood seasonal pastures. Because movement is now severely constrained by dense settlement and livestock herds all round the swamps, Nile Lechwes tends to converge on levees and termitary complexes within the toic until the floods begin to subside in about October. By the time fires are burning the floodplain (January–March), the animals are occupying the patchy margins of the permanent swamp, where they avoid Papyrus but are commonly found in Sudd Grass. At this time competition for grazing is keen and large herds of cattle tend to force the Nile Lechwes deeper into the swamps.



Nile Lechwe adult male in pursuit. At a distance the white nape draws attention to the length of the horns.

FOOD Grazes on growing *Oryza* during the early flood season but mainly *Leersia*, *Echinochloa* and *Vossia* as the floods recede.
BEHAVIOUR Females determine movements but spaced-out, fully adult, piebald males drive competing males away from female groups. In the early dry season (November–December) single males successfully exclude other piebalds from herds that can be in excess of 100. This is the period of peak births. By February calves have emerged from lying-up in the reeds and sometimes gather for playful chases, circling and jumping through the shallows. As females move, gathering and fragmenting into larger and smaller groups in response to the state of the pasture or disturbances, they attract the attentions of piebald males. By March these males are spaced out in a rather linear scatter along the swamp margins and there is much sexual activity that would seem to peak in about April. Piebald males often tolerate the presence of several other well-horned males in their vicinity but these can always be graded by colour and clearly represent hierarchically ordered age-classes. Dominant males squirt urine onto their own throats, which may then get rubbed onto females. Because actual horn-to-horn engagements often submerge heads, male fights in water tend to be brief tests of strength with very vigorous pushing and wheeling. Once the loser breaks away there is a token chase and the winner returns to the females (if present). Exhausted males seclude themselves in trampled arenas within the reedbeds. Males may utter squeaky grunts while fighting. Females are extremely vocal and there are choruses of toad-like croaking in herds that are actively on the move. Gestation has not been recorded but is probably about 8 months. Longevity is also not known but, given the slow, graduated maturation of males, probably resembles the Southern Lechwe's 15 or more years.
ADAPTATIONS The male's bold black-and-white colouring is probably made possible by a scarcity of predators on very extensive floodplains. Crocodiles and pythons are known to take them but these predators do not hunt by sight. It may be significant that the one Southern Lechwe population in which the males are black also lives on a very wide, flat floodplain with few resident predators. Colour-coding for age-ranks assists hierarchies while marked differences between males and females would appear to allow each sex to pursue an independent life cycle. Males head-flag at the boundaries between their very ephemeral territories. Flagging involves sudden sweeping tosses of the head (as if to chase a fly off the flanks). This violent movement momentarily exposes the white ears, neck and shoulder patch and flourishes the horns. This intimidation display helps define temporary boundaries through repetitive stand-offs.
STATUS About 16,000 Nile Lechwes lived on the east bank of the Nile in 1983. A similar number has been estimated for the west bank. Nearly 1,000 have been estimated for the Machar marshes. Although constrained by competition from cattle, and subject to some hunting, numbers are probably stable. Plans to resuscitate the Jonglei Canal, introduce irrigation or exploit oil could dramatically change this. Listed as threatened (IUCN).

WATERBUCK *Kobus ellipsiprymnus*

OTHER NAMES Fr. *Cobe defassa*. Ger. *Wasserbock*. Swah. *Kuru*.
MEASUREMENTS HB 1.77–2.35m. T 330–400mm. Sh. ht 1.20–1.36m. W 160–200kg (♀), 200–300kg (♂).
RECOGNITION A big, shaggy animal, rather variable in colour, with dark grey and rufous individuals sometimes occurring in mixed groups. Males tend to be darker and have long horns (500–990mm). Females are without horns and tend to be warmer in colour. The angle of the chin, muzzle, ears and eye-surrounds are white, with black margins and tips to the ears. The dark legs also have short white spats.
GEOGRAPHIC VARIATION Common Waterbuck *K. e. ellipsiprymnus* (SE Africa): white rump crescent. Defassa Waterbuck *K. e. defassa* (NE, central and W Africa): all white under tail.

DISTRIBUTION Well-watered valleys, mainly in tropical Africa and sandwiched between desert and forest. Absent from the dry north, north-eastern and south-western regions of Africa.

HABITAT Sedentary in savannas, woodlands and forest/non-forest mosaics where there is permanent water. They favour woods or thickets, where they inhabit the fringes of valley grasslands. They could be described as 'dry-land lechwes'.

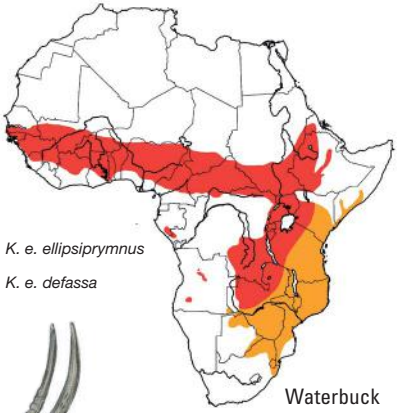
FOOD Many grass species, including reeds and rushes (*Phragmites* and *Typha*). Where green grass is scarce, Waterbucks may browse leaves or even fruits.

BEHAVIOUR Both males and females remain for long periods (up to 8 years) on the same home-range. Females travel over the larger areas (typically 200–600ha) but travel contracts with age. Males are most vigorous between 6 and 10 years of age, when they hold the largest territories (ranging from 4 to 146ha), with continual change and readjustment as the relative status of neighbours waxes and wanes. Familiar males that appease territory-holders are tolerated. Females travel at will over many territories, usually in ones and twos but sometimes assembling in temporary aggregations of up to 70. Young animals go through a stage of being chased and may emigrate to distances of up to 30km.

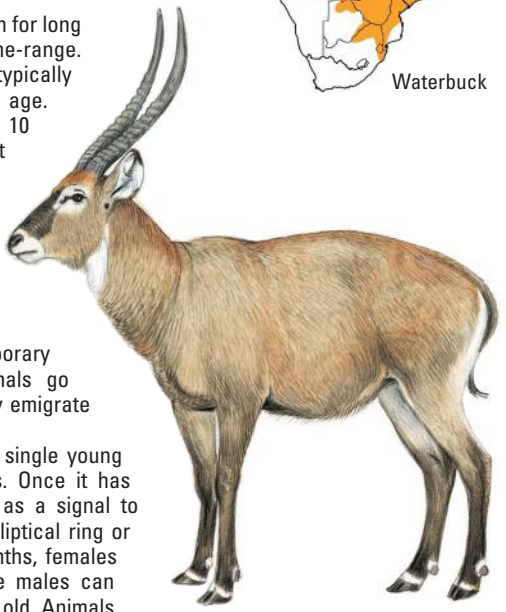
Gestation lasts over 8 months and the single young remains concealed for at least 2 weeks. Once it has joined its mother her raised tail serves as a signal to follow (the signal is emphasised by an elliptical ring or wholly white buttocks). Weaned at 6 months, females generally mature at about 3 years while males can scarcely compete before they are 5 years old. Animals are known to live for 18 years.

ADAPTATIONS Scent is clearly of paramount importance for Waterbucks and their own odour is so strong that it can sometimes be detected at a distance by the human nose. Partly or wholly uneaten kills by Lions have led to the suggestion that they are distasteful but this is contradicted by the fact that Lions, hyaenas and other large predators will kill Waterbucks more frequently than their abundance would merit. It would appear that this is the price they pay for being easy to find by other Waterbucks. The benefits of living both in herds and being able to come and go, assemble and dissolve, in response to an unstable environment appear to outweigh the extra risk from predators.

STATUS Although Waterbucks have been eliminated from many localities in their very extensive range they remain widespread and well represented in parks and reserves.



Waterbuck



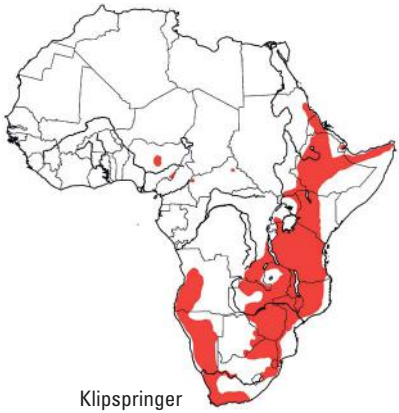
Defassa Waterbuck *K. e. defassa*

Rear views of female *K. e. ellipsiprymnus* (*above right*) and male *K. e. defassa* (*right*).

KLIPSPRINGER Oreotragini

A unique type of basal antelope with a fossil of the extant species from 1.6 mya. Klipspringers are most likely to have evolved on the Ethiopian massif. Digital bones and hooves have been uniquely modified for traversing over rocky surfaces. Being a long-established and conservative lineage with widely separate populations, arguments have been made for multiple species. These are treated as subspecies here because observable differences between them are very minor, mostly featuring subtle gradations in the tinting of their pelage.

KLIPSPRINGER *Oreotragus oreotragus*

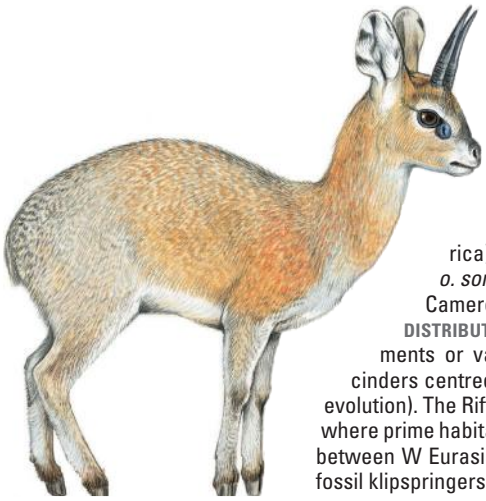


Klipspringer

OTHER NAMES Fr. *Oréotrague*. Ger. *Klippspringer*. Swah. *Ngurunguru, Mbuzi mawe*.

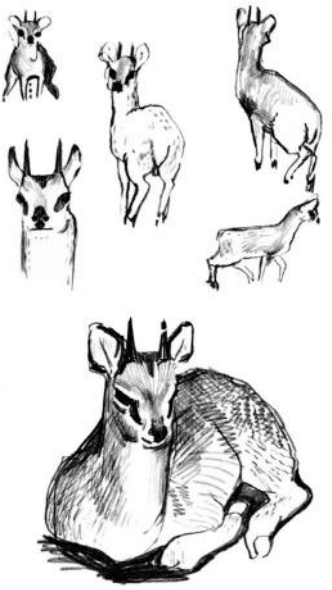
MEASUREMENTS HB 750–1,150mm. T 65–105mm. Sh. ht 430–600mm. W 8–18kg (average weights vary regionally, 10–15kg).

RECOGNITION A small, compact antelope, unique for walking and jumping on the tips of its hooves and for its dense cloak of lightweight fur, which is brittle, coarse and rustles when shaken or touched. This fur gives the illusion of greater size, especially when erect (when the animal is hot or sick). Widely spaced eyes behind a contracted and narrow muzzle give the animal a short, wedge-shaped face and binocular vision. There are strong regional differences in colouring but also much individual variation. Animals from the arid north-east are a creamy yellow, graduating into grey on the legs, with pale sepia hocks. Ethiopian populations are less bleached but similar. Bold colour contrasts and patches of softer fur are most apparent in animals from humid uplands of central and SE Africa. In East Africa boundaries between yellowish north-easterners and russet-shouldered central African animals become blurred and both colourings co-exist. The Zambezi marks the northern margin of southern African forms. The Klipspringer only signals from 'the front end' and displays none of the tail-wagging so typical of other small antelopes. Instead, its black-edged ears have tracts of white fur that readily catch the eye when flicked. The males have short, upright horns and in some populations (Tanzania, Uganda, Ethiopia) there is a high incidence of horned females. Their horns are generally no more than 90mm long but male horns of 160mm have been recorded.



GEOGRAPHIC VARIATION *O. o. oreotragus* (coastal regions of far south and Cape), *O. o. tranvaalensis* (upland South Africa and Drakensberg), *O. o. tyleri* (Namibian escarpments and uplands), *O. o. aceratos* (SE Africa between R. Rufiji and R. Zambezi), *O. o. centralis* (south-central Africa), *O. o. schillingsi* (East Africa), *O. o. saltatrixoides* (Ethiopian highlands), *O. o. somalicus* (N Somalia), *O. o. porteousi* (Nigeria/Cameroon, Central African Republic).

DISTRIBUTION Mostly steep, rocky hillsides, escarpments or valleys or open screes of loose pebbles or cinders centred on Ethiopia (the most likely centre for their evolution). The Rift Valleys link this region with southern Africa where prime habitats are also extensive. Numerous exchanges between W Eurasia and Ethiopia help explain the presence of fossil klipspringers outside Africa some 5 mya.



Klipspringer

Animals can withstand day/night temperature fluctuations swinging from 42° C in the shade to freezing. This ability is clearly due to the insulating effect of their hollow-shafted fur. Klipspringers occur up to 4,000m on Mt Kilimanjaro and on the summit of Mt Meru (4,500m), where frost and snow are frequent.

HABITAT The very varied habitats and latitudes in which Klipspringers are found have two features in common: rocky, stony ground and abundant short vegetation. Food rather than cover is the crucial resource. Where drought or fire temporarily deprive them of food they tend to move down to escarpment or even valley bottoms. At such times Klipspringers also abandon their territorial behaviour. Over most of their range they are greatly outnumbered by hyraxes, which are presumably their main competitors for food resources.

FOOD Herbs and low foliage are the main items throughout the range, with green grasses mainly a wet-season food. In Ethiopia grass forms about 17% of the annual diet while herbs account for more than half, and bushes, shrubs, and creepers the rest. In some areas, seeds, fruits, buds, twigs and bark are important seasonally; ephemerals such as *Vellozia* lilies can be temporary staples. Food distribution, temperature and disturbance all influence the duration and times of feeding. Klipspringers generally rest during the heat of the day and after midnight. Moonlight invites more activity than dark nights. Early morning sunning is important at high altitudes.

BEHAVIOUR It is rare for Klipspringers to remain solitary for very long. A female is generally attended or followed by a male and she commonly has a young one or an adult offspring with her or nearby. Males are much more vigilant than females. This may have benefits in spotting predators but appears to be primarily directed at keeping other males away. Pairs are permanently resident in territories that range from 7.5 to 49ha. Males remain almost continually aware of their female's whereabouts and 'duets' of whistling are a means of regaining contact after any disturbance. Mutual face-rubbing follows each reunion. Whistles also advertise territory and are an immediate response to predators. Conspicuous fluctuations in the size of facial glands have been observed to coincide with heightened sexual behaviour.

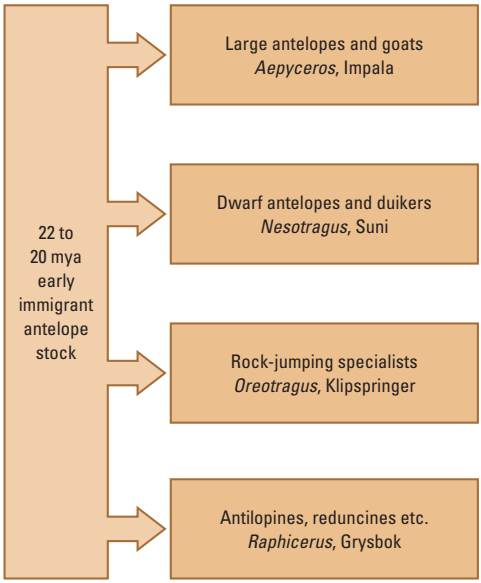
Mating peaks are recorded from several areas. After the lengthy gestation of several months a well-developed young is born and immediately hides. Only visited three or four times a day for suckling, the kid tends to remain a hider for up to 3 months. Over that period it gradually increases the time it spends with the mother. This prolonged hiding may be a response to heavy predation from the eagles that are very abundant in Klipspringer country (which is also hyrax country). Females are sexually mature at 1 year, males somewhat later, passing through a 'dispersal' phase during which they have no territory. Klipspringers are known to live for 15 years.

ADAPTATIONS Moisture and nutrients on eroding hillsides and cliffs support a rich vegetation that is not accessible to herbivores without special skills in negotiating rocks and screes. The time required to evolve appropriate capabilities handicaps latecomers and favours pioneers. Conservative traits in Klipspringer cranial anatomy suggest that their ancestors derived from the very earliest stock of African antelopes. Feet and hooves have gradually modified to the point at which no later bovids can compete. Even the Ibex, a late colonist from Eurasia, has not displaced the Klipspringer in Ethiopia.

STATUS An incapacity to escape local vicissitudes and very limited ability to disperse or recolonise lost ground suggests that the Cameroon model (steady shrinkage to vestigial proportions) will overtake other populations unless active reintroductions to suitable habitats are initiated. With careful management the survival of this species could not only be assured but improved. Listed as endangered (IUCN) in Cameroon, Nigeria and Uganda but not endangered in other parts of their range.

IMPALA Aepycerotini

Virtually unchanged in 5 million years, and with a suggestive ancestral fossil at 14 mya, the Impala has a number of significant adaptations. Its special evolutionary significance is that this seems to be the sole survivor of an 'enlarged dwarf' lineage that eventually gave rise to several other large-bodied lineages, notably alcelaphines, hippotragines and caprines.



Four antelope radiations over the last 20 million years and the most conservative surviving genus in each.

IMPALA *Aepyceros melampus*

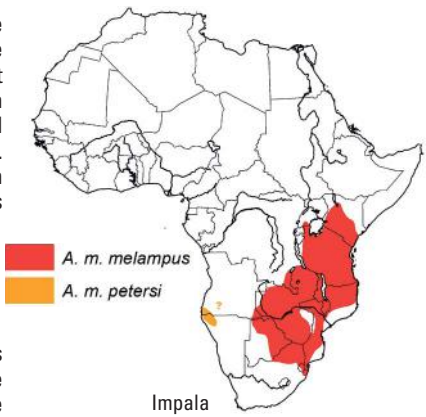
OTHER NAMES Fr. *Impala*. Ger. *Schwarz Fersen Antilope*. Swah. *Swala pala*.
MEASUREMENTS HB 1.2–1.6m. T 300–450mm. Sh. ht 750–950mm. W 400–600mm (♀), 450–800mm (♂).
RECOGNITION A medium-sized gazelle-like antelope with a brown or yellowish-brown back that becomes lighter on haunches, shoulder, neck and head, and sharply lighter on the flanks. Underside, chin, mouth and ear linings are white. Ear tips, thigh stripes, midline of tail and back, and bushy fetlock glands are black (there are bold black eye-stripes and a black bridge to the nose in an isolated Namib population). Adult males have long, narrow horns, with shallow, well-spaced annulations, that arch up and out then back and up.

During rutting the necks of males thicken, their coats become darker from the grease of sebaceous secretions and they acquire a musky scent. There are no preorbital glands but the entire forehead is glandular and fossils reveal preorbital pits in ancestral forms.

GEOGRAPHIC VARIATION Common Impala, *A. m. melampus* (SE Africa). Black-faced Impala, *A. m. petersi* (SW Africa): a relict population with several conservative features – sometimes treated as a species.

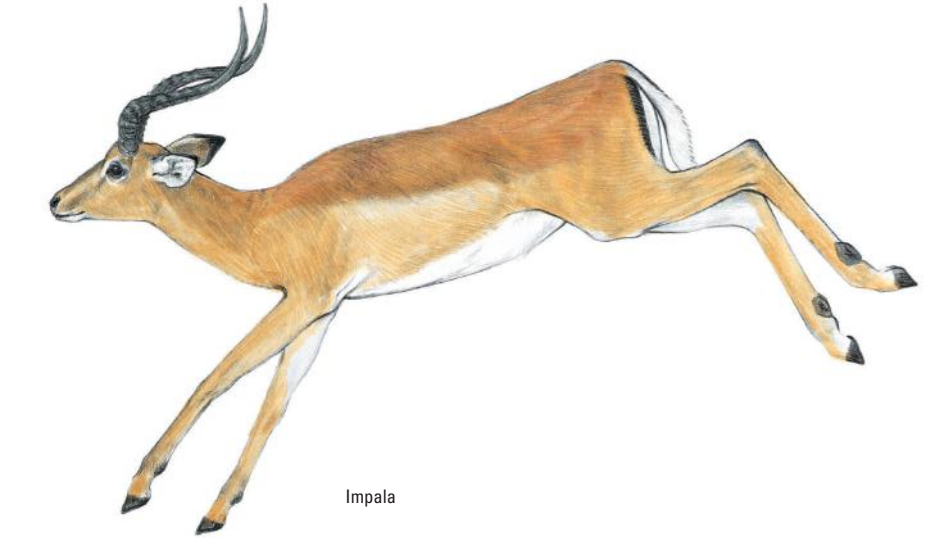
DISTRIBUTION A patchy scattering from Kenya south to the Transvaal, Botswana and E Angola. The Black-faced Impala is an isolated population in SW Angola and a small area of Namibia.

HABITAT 'Edges' between grassland and denser woodlands, notably *Acacia*, are preferred. They require high-quality fodder (whether grass or leaves), moisture, shade and cover. This unstable mosaic is characteristic of SE Africa, where Impalas are known to have been present for at least 4 million years. In favourable localities numbers can reach more than 200 per km^2. Grassland is occupied during the rains, woodland more in the dry season. Adult males have a greater tendency to remain in denser vegetation than females. In all areas Impalas are highly residential, seldom moving more than 10km and even then only temporarily.



Impala

FOOD Almost wholly grazers during the rains. The amount of grass in the diet drops to about 30% in the dry season, when Impalas are mostly in the woodlands, browsing on shrubs, herbs, pods and seeds. *Acacia*, *Combretum* and *Grewia* are important in most areas. Feeding usually takes place



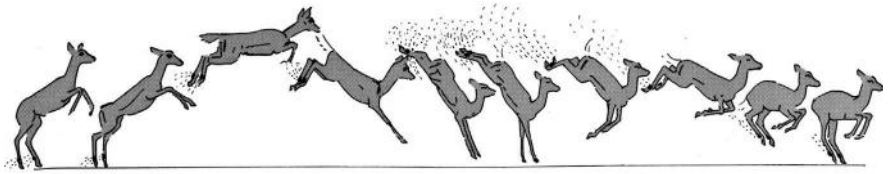
Impala

in two major bouts (around dawn and dusk) and two minor bouts (midnight and early afternoon), with shading and ruminating in between.

BEHAVIOUR Recent research has shown that females form 'clans' of 30–120 animals with home-ranges radiating out from fairly stable centres but extensively overlapping the ranges of neighbouring female clans. From such centres year-round movements may extend for about a kilometre but core ranges have been estimated at 80–180ha. Although gregarious, neither females nor males form any lasting associations (not even with their young).

Male offspring share their mother's home-range but begin to wander more widely as they mature (shifting their focus up to 4km away from the mother's range). Full horn and neck development is reached by males at about 4 years but the intolerance of other males restricts their movements and forces them to defend themselves within an area much smaller than their parental home-range. Their attachment to this area becomes more marked with age. The nature of their 'tenure' changes or cycles with their own hormonal condition and with that of other males that share part or all of their home-range. Most healthy adult males become intensely intolerant of other males when in the presence of oestrous females. This intolerance is expressed in direct challenges and fights during the rut. In southern Africa the rut lasts only a few weeks and, since males are almost continually inspecting, herding and copulating with females, confronting other males or rushing around roaring and chasing, they are soon exhausted and capitulate to fitter males. At the highest densities any single male's tenure of a 'territory' is ephemeral, lasting only 3–13 days.

If both the boundaries and the tenure of male territories appear unstable this is because being excluded or becoming an excluder depends on the presence and sexual condition of females. Mating peaks coincide with the rains in both southern and tropical Africa, but in the latter region two seasonal peaks are very much less sharply defined. One young is born in a secluded spot after a gestation of about 200 days. The mother remains nearby and visits only to suckle it. After some



Impala female leaping and making 'empty kicks'.

days the young begins to follow but seeks shelter at the least alarm. About half of all young are lost to predators within the first few weeks. Females are sexually mature in 18 months and animals live for up to 15 years.

ADAPTATIONS Fetlock glands, unique to Impalas, assist the laying of trails, presumably by helping temporarily detached or 'lost' individuals to find company. This function relates not only to trails left while walking; high kicks (another Impala peculiarity) send out puffs of scent that may help dispersed animals to regroup after a scare. Roaring of males allows them to space themselves acoustically, to intimidate potential rivals and assess risks with respect to other males within a wooded environment.

STATUS Widely distributed, fecund and well represented in numerous national parks, Impalas are vulnerable or endangered only on the outer margins of their range, as in Uganda and Rwanda.

ALCELAPHINES, TOPI AND ALLIES Alcelaphini

Hirola	*Beatragus hunteri*
Bontebok/Blesbok and Topi	*Damaliscus* (2 species)
Hartebeest	*Alcelaphus buselaphus*
Gnus	*Connochaetes* (2 species)

RECOGNITION Alcelaphines have a long face and legs, double-curved, hollow horns, fast gaits and a part or wholly grass diet in common. The Hirola resembles many other antelopes (and even deer) in its dimensions. The larger Topi, Hartebeest and wildebeest (gnus) have diversified into more distinctive types. The Impala was previously judged to be a primitive alcelaphine but this has proved to be too restrictive of its larger significance and it now occupies a tribe of its own. Its resemblance to the Hirola serves as a reminder that the larger species have evolved relatively recently from smaller ancestors.

GENEALOGY Most of the alcelaphine peculiarities were already present, albeit in a less marked form, in both fossil ancestors and in their modern descendants. Alcelaphines emerged late (less than 8 mya) and their fossil remains demonstrate very rapid change. Their hollow horns and forehead permit remodelling of the skull so that closely related forms can easily acquire very different horn shapes. The hammer-shaped head of the Hartebeest is due to a bending of axes, the muzzle tipping downwards while the horns twisted round (as is revealed by a good fossil series) until their hooked tips were literally 'back to front'.

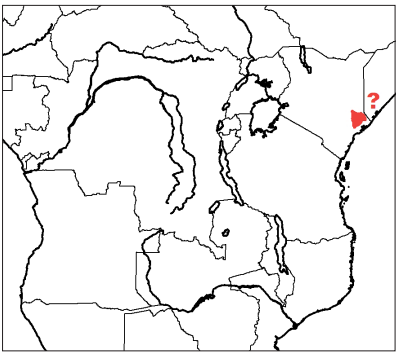
GEOGRAPHY Alcelaphines evolved in Africa and were very successful. Some early forms spread out to India but later became extinct there. Advanced, water-dependent grazers, they have always been most abundant and diverse on the eastern side of Africa. Nonetheless, their recent range included the North African littoral, the West African savannas and the Horn, where they lived in immense numbers on a variety of pastures. Most of these populations belonged to the Hartebeest group, *Alcelaphus*.

ECOLOGY Alcelaphines are grazers adapted to live at high density on a very abundant but unstable food supply. They tolerate substantial seasonal fluctuations but few do well in really arid habitats. Exposure on open plains has selected for great speed and stamina.

NATURAL HISTORY As high-density grazers living in close proximity, alcelaphines have evolved advanced, but somewhat unusual, social systems dependent on scent-marking of bodies rather than sites in the environment. All have retained very active pedal scent glands and most species kick, stamp or cavort to disperse scent during social displays. The combination of an intensely competitive social life and a capacity for great speed means that a number of displays are performed on the run, such as ritualised gaits, prances and postures.

ADAPTATIONS The usual effect on limbs of increasing body weight is for them to become proportionately shorter and thicker. However, the larger alcelaphine species have retained fast gaits, long legs and a heavy, muscular body, but without elongating the neck in proportion. This disproportion has therefore led to a long face that is able to reach the ground. The short, muscular neck is an essential adjunct to the frequent horn-fighting necessary in a high-density, competitive society.

HIROLA *Beatragus hunteri*



Hirola

OTHER NAMES Fr. *Antilope hirola*. Ger. *Hirola*. Swah. *Hirola*.

MEASUREMENTS HB 1.20–2.0m. T 300–450mm. Sh. ht 1.00–1.25m. W (est.) 80–118kg.

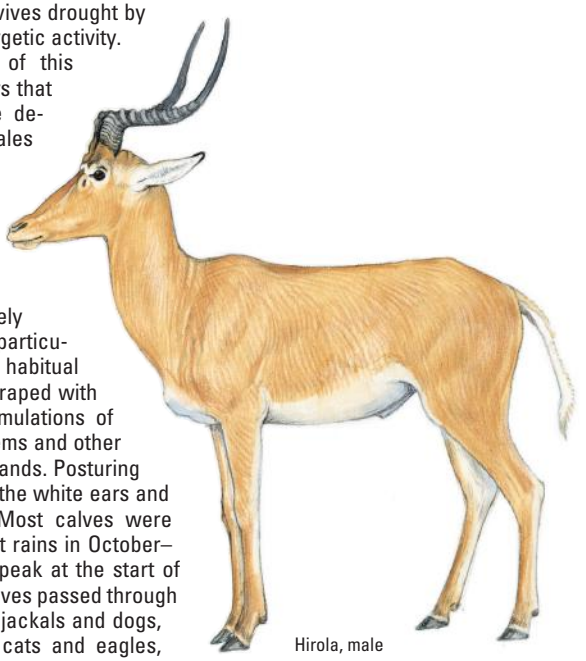
RECOGNITION An antelope with unusual proportions and colouring, of medium weight, with long legs and a long body but a relatively short neck and a long face. The lyrate horns are not unlike those of the Impala but have less flare and much heavier bases with pronounced annulations. The uniform sandy colouring gives way to a slaty grey in older males. The long tail and black-tipped ears are startlingly white, as are the 'spectacles' around the eyes (patterns that emphasise the eyes are typical of some kob types but most antelopes have a dark 'mask' that conceals the eyes). The structure of its large preorbital gland and muzzle differs from that of the Topi and Hartebeest. Pleistocene *Beatragus* was substantially larger.

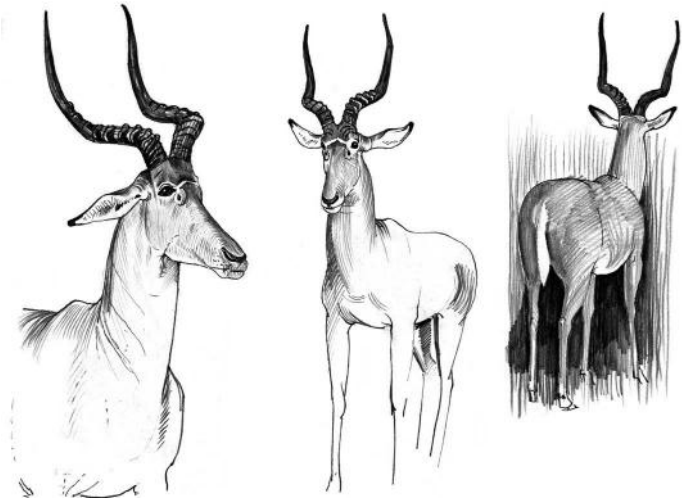
DISTRIBUTION Since the mid-Pleistocene, less than 1 mya, the emergence of more advanced, high-density grazers, Hartebeest, probably contributed to the Hirola's steady decline. Whatever its history, it is now confined to a rapidly shrinking corner of SE Kenya (it no longer survives in Somalia).

HABITAT A narrow strip of seasonally arid, grassy plains sandwiched between the waterless *Acacia* bush of the hinterland and forest–savanna mosaic on the coast (desert and thicket barriers might have served to exclude Hartebeest from this area). The northern margins of its range coincide with a type of very dry *Acacia* scrub where the grass cover becomes very much more sparse. Richer pastures used to be shared with moderate numbers of other grazers.

FOOD Strictly a grazer, feeding on the dominant grasses, notably species of *Chloris*, *Cenchrus* and *Digitaria*. The large molars are well suited to chewing such coarse grasses. It feeds most intensively in the early morning and evening. Able to go without drinking, it also survives drought by laying down fat and avoiding energetic activity.

BEHAVIOUR The last individuals of this species exist in such low numbers that their natural behaviour must be described in the past tense. Females with young formed groups numbering between 5 and 40, often attended by a single territorial male. All-male groups were common, occasionally associated with Topi males. Herds were thought to be relatively sedentary and solitary males particularly so. Such males postured on habitual stamping grounds, which they scraped with the feet and marked with accumulations of dung. They also marked grass stems and other vegetation with their preorbital glands. Posturing included head-flagging, in which the white ears and spectacles were conspicuous. Most calves were born at the beginning of the short rains in October–November, suggesting a mating peak at the start of the main rains in March–April. Calves passed through a very vulnerable stage in which jackals and dogs, as well as hyaenas, the larger cats and eagles,


Hirola, male



Hirola, adult male frontal and rear views

might all have been significant predators. The Hirola's lifespan is not known but capture experiments revealed that it was subject to muscular dystrophy. Delicacy during capture might have been due to a lowered metabolism in the dry season.

ADAPTATIONS A peculiarity of the males is the very thick skin of the nape (a necessary protection against the sharp horns of rivals during fights), which folds up behind the horns when the ears are pricked. Animals apparently fight on their knees when in earnest and in a standing position when sparring.

STATUS IUCN has classified this species as critically endangered. In its last (nominally protected) reserve there are now 232 sheep, goats, cattle and camels for every one Hirola. An intensive aerial survey in 2011 yielded a count of 245 individuals. It is extremely unlikely that this unique and beautiful animal can now survive. Yet, as recently as 1981, the population was estimated at 16,000 animals. Any chance of survival would have depended upon protection, and exclusion of the vast livestock holdings of the region from the 533km^2 Arawale Reserve which was specifically designated for Hirola. Medieval local livestock interests are fiercely aggressive and will never allow this to happen. Outside, in Tsavo NP, a small herd introduced in the 1960s and another in 1996 are only just managing to sustain their numbers in the face of regular Lion predation. Both situations illustrate the true process of extinction in our time, as at any other time.

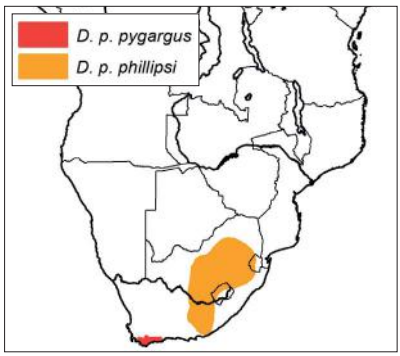
BONTEBOK/BLESBOK

Damaliscus pygargus

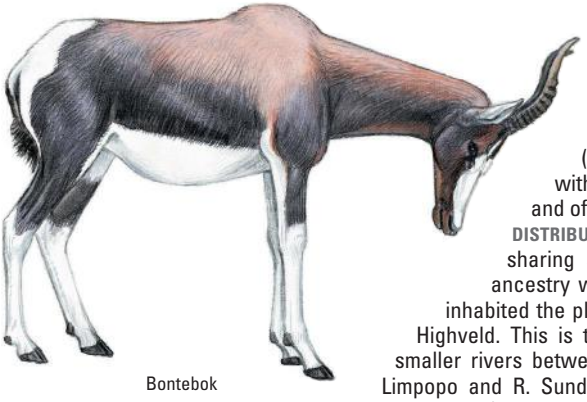
OTHER NAMES Fr. *Bontebok, Blesbok.*
Ger. *Buntbock, Blessbock.*

MEASUREMENTS HB 1.4–1.6m. T 300–450mm.
Sh. ht 0.85–1.0m. W 55–70kg (♀), 65–80kg (♂).
Bontebok an average 8kg lighter.

RECOGNITION Smaller southern cousins of the Topi, with very strong contrasts of colour in adults but fawn young with completely different, gazelle-like colouring. They have a compact body, short neck and a long nose with an expanded muzzle. Their horns resemble enlarged gazelle horns. The tail is short with a black, tufted tip. The differences between subspecies are given below.



Bontebok/Blesbok



Bontebok

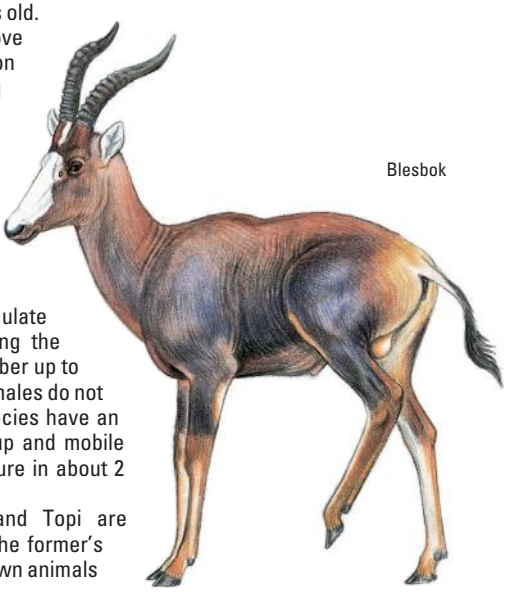
GEOGRAPHIC VARIATION Bontebok, *D. p. pygargus* (W Cape): glossy dark purplish-brown with white buttocks and 'stockings'; very dark horns. Blesbok, *D. p. phillipsi* (Highveld): dull reddish brown with ill-defined off-white buttocks and off-white lower legs; paler horns.

DISTRIBUTION South African isolates sharing a geologically recent common ancestry with Topi. The Blesbok formerly inhabited the plateau grasslands known as the Highveld. This is the watershed for innumerable smaller rivers between the larger valleys of the R. Limpopo and R. Sundays. 'Sweepstake' colonisation of the Cape (probably across the Nieuwveld range and within the last few thousands of years) led to physical and genetic isolation of the Bontebok. Derived from a small number of founders, it was unlikely to have been widespread, even before the arrival of humans with livestock.

HABITAT The Blesbok originally ranged over the entire Highveld, grazing the fire-climax grassland dominated by Red Oat Grass, *Themeda*. The Bontebok inhabited a different Cape fynbos habitat where grassy areas were scarcer. In both parts of their range, animals had regular access to water.

FOOD Red Oat Grass, *Themeda triandra* (at various stages of growth), *Eragrostis* and *Chloromelas* form the main part of the Blesbok's diet. A species of *Setaria* is taken only in winter and there are seasonal changes of pasture. The Bontebok also feeds on *Eragrostis* species but local dominants, *Bromus* and *Danthonia*, are the preferred grasses.

BEHAVIOUR The Blesbok formerly tended to migrate between seasonal pastures, forming huge mixed herds in the autumn and winter. Where the pastures in modern enclosures are sufficiently extensive to support them Blesboks still gather in semi-nomadic herds. Even in smaller groups within still smaller enclosures both subspecies retain the habit of circulating around their available range in loose herds. The membership and numbers of these mobile aggregations are unstable but include sexually inactive males and younger, but independent females less than 2 years old. Adult females with offspring tend to move over much smaller areas, a restriction reinforced by the territorial males living there. These males have focal centres to their territories which are marked with dung and urine on middens. Although the spacing between males varies greatly, their inner core of 'markable' and 'defendable' territory is always less than 5ha. Female Bonteboks seldom gather in groups of more than 10 (including their young) and they circulate over two or three male territories during the February rut. Blesbok female groups number up to 25 and mating peaks in April. Pregnant females do not leave the herd to give birth. Both subspecies have an 8-month gestation and their young are up and mobile within an hour or two of birth. They mature in about 2 years and can live for up to 17 years.



Blesbok

ADAPTATIONS The young of Blesbok and Topi are apparently identical at birth except for the former's smaller size. Both begin as pale, sandy-fawn animals

with creamy undersides. First the bridge of the nose darkens, then dark leg and flank stripes (like those of Springboks or gazelles) begin to extend over the sides and limbs. This darkening proceeds until there are more or less separate black patches in tropical Topi. Pale undersides become ochre-coloured in Topi, white in Bontebok. The pale root to the tail is very similar in some Topi and Blesbok. As the Bontebok matures this cream-coloured area turns white and forms a sharply defined genital beacon. In both Blesbok and Bontebok the bridge of the nose becomes the badge of maturity. As their horns lengthen it turns white with crisp black borders against the sides of the face. Most Topi keep a black nose but rare individuals switch colours as they mature and have white blazes as conspicuous and of the same shape as those of the Bontebok. These transformations during the development of individuals and the variation evident even in today's impoverished herds illustrate the potential for rapid differentiation in isolated populations.

That Blesbok and Topi have diverged very recently is shown by a perfect intermediate form, a supposed common ancestor, being very common in both southern and eastern African fossil deposits that are less than 1 million years old. *Damaliscus agelaius* was similar in size to the Blesbok, suggesting that this lineage has become more than twice as heavy in the rich sumplands of the tropics while their southern counterparts on the leached Highveld have remained more conservative. One reason for their divergence may have been the emergence of a new competitor, the Hartebeest, taking over as dominant grazer in dry savanna grasslands.

STATUS The Blesbok is now commercially ranched livestock and very few occur in formal conservation areas. The Bontebok is also kept on farms (one having been made into a national park). Although both are now extinct as wild animals their survival is now more secure.

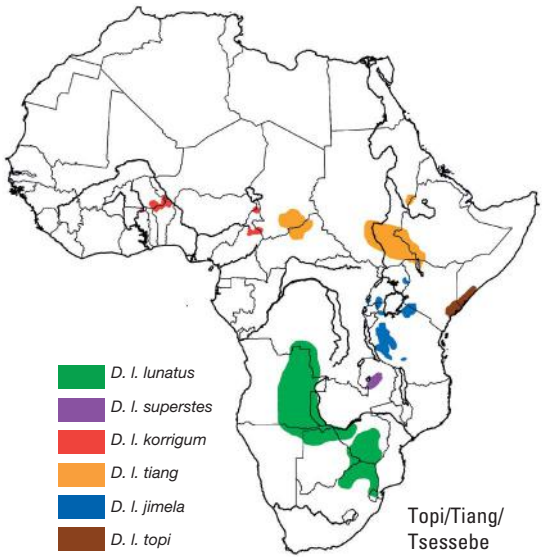
TOPI/TIANG/TSESSEBE

Damaliscus lunatus

OTHER NAMES Fr. *Damalisque*. Ger. *Leierantilope*. Swah. *Nyamera, Topi* (at least two of the local names are synonymous with 'mud', reflecting these animals' sumpland habitats).

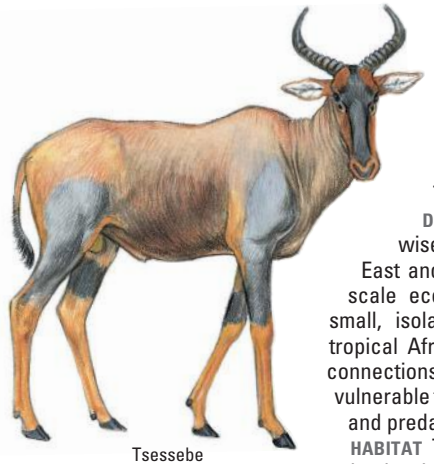
MEASUREMENTS HB 1.5–2.3m. T 360–420mm. W 75–150kg (♀), 120–160kg (♂).

RECOGNITION A large, compact antelope with a deep chest, prominently ridged shoulders, a rather short neck and a long face. The tail is narrow and fringed. Horns vary from one region to another in their splay and arching but all have backward-curving stems and forward- or inward-curving tips. The body colour varies from rather yellowish, bleached brown to red or even purplish brown. There are black patches on the hindquarters and forelegs above ochre-coloured 'stockings'. The bridge of the nose is black (very occasionally turning white with maturity). The coat of healthy animals is always tight and very glossy. The hooves are narrow and splay out on soft ground.



Topi/Tiang/ Tsessebe

GEOGRAPHIC VARIATION *D. lunatus* is recently evolved but climatic vicissitudes within each separate sump result in periodic boom/bust population crashes followed by genetic founder-effects in the survivors. This probably helps explain rapid differentiation within each separate sumpland region. This ecological history has failed to influence the Phylogenetic Species Concept doctrine that regards any perceptibly different population as a species. Proponents of PSC taxonomy have proposed that each of 10 sumpland populations is a full species. That course is not followed here, but six subspecies are recognised as follows:



Tsessebe
D. l. lunatus

Tsessebe, *D. l. lunatus* (southern Africa);
Bangweulu Tsessebe, *D. l. superstes* (NE Zambia);
Korrigum, *D. l. korrigum* (Senegal to W Nigeria);
Tiang, *D. l. tiang* (NE Nigeria to W Ethiopia);
Nyamera, *D. l. jimela* (Great Lakes region);
Topi, *D. l. topi* (E African coast).

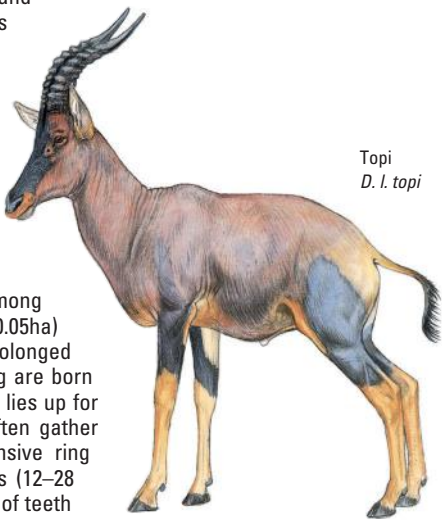
DISTRIBUTION Sumplands and floodplains in otherwise relatively dry regions south of the Sahara, East and central Africa. All populations centre on large-scale ecosystems and they are absent from the many small, isolated floodplains that are scattered throughout tropical Africa. Although there must have been continuous connections in the past, small isolated groups appear to be vulnerable to vicissitudes of climate (and possibly competition and predation).

HABITAT These antelopes live in seasonally flooded grasslands where they follow receding waters in the dry season and retreat onto slightly higher ground in the rains or flood season. Failed rains or floods can lead to very extensive die-offs.

They favour naturally short or medium-height pastures (such as alkaline pans), regrowth after burns or else concentrate in large herds in tall grass (commonly on wet-season higher ground retreats). Here heavy trampling soon opens up large glades and stimulates continuous regrowth. These annual cycles of movement can involve huge herds of tens of thousands in round journeys of nearly 1,000km, small circuits within closed valleys, or sustained residence on 'permanent' pockets of suitable grassland. The instability and unpredictability of floodplain pastures renders the last group peculiarly vulnerable. The advantages of living in very large, mobile herds include reduced predation and optimum grazing, partly due to their own trampling. Younger animals benefit from older animals' knowledge of the region's pastures.

FOOD Most valley grasses are taken. Longer rather than very short leaves are stripped from the stems with a nodding action that finely balances raking wrenches with clipping bites.

BEHAVIOUR Although many Topi live in large migratory herds, they may be neighbours to (or co-exist with) small clusters of residential animals. The residential animals are probably offshoots of the larger aggregations but display different behaviour in that they occupy territories defended by males (and sometimes also by females). Scattered residents tend to be less seasonal in their breeding. Large groups instead tend to have very intense periods of rutting while herds are at their most concentrated. In some areas mating may take place 'on the hoof' but in most instances it tends to focus on territorial clusters. Close proximity may stimulate hormones in both sexes and the build-up of scent in particular 'hot-spots'. Males fight for access to oestrous females, who are probably drawn in by the scent. Competition among males results in ever smaller territories (down to 0.05ha) where all the elaborate preliminaries of prolonged courtship are abbreviated and intensified. Young are born after an 8-month gestation. The sandy-fawn calf lies up for a few days before joining its mother. Young often gather spontaneously and females may form a defensive ring around them. The age of sexual maturity varies (12–28 months in females, males up to 42 months). Loss of teeth



Topi
D. l. topi

after about 15 years results in death. Females are fertile to the end and bear young even as the last roots of their teeth fall from their jaws.

ADAPTATIONS Adaptation to living on floodplains appears to be relatively recent in Topi as their feet are only slightly modified for walking in soft soils. It is possible that ancestral Topi ceded the greater part of a formerly more extensive grass-eating niche to the larger Hartebeest which is a more recently evolved, more advanced grazer. Greater speed, stamina, mobility and versatility enable the Topi to compete with the kobs, lechwes and Waterbuck. **STATUS** Topi have been eliminated from the greater part of their range but can still reach very high densities in their remaining refuges. Currently well represented in reserves and national parks of eastern and southern Africa.

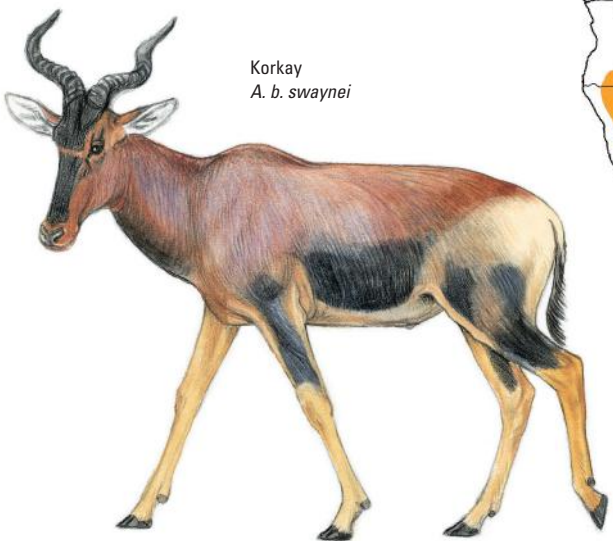
HARTEBEEST *Alcelaphus buselaphus* (incl. *lichtensteinii*)

OTHER NAMES Fr. *Bubale*. Ger. *Kuhantilope*. Swah. *Kongoni*.

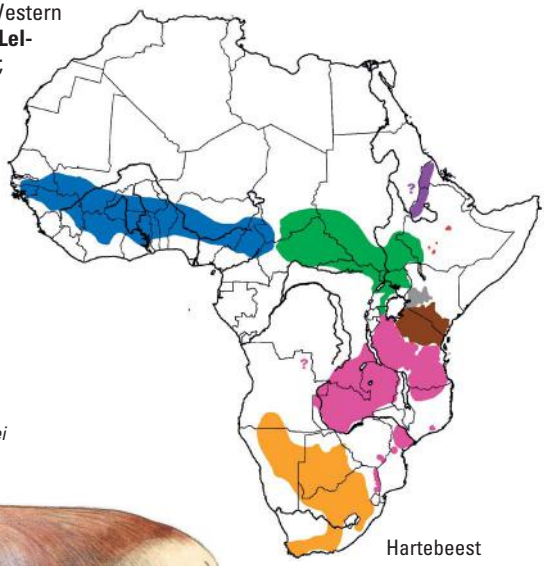
MEASUREMENTS HB 1.60–2.15m. T 300–700mm. Sh. ht 1.07–1.50m. W 116–185kg (♀), 125–218kg (♂).

RECOGNITION A large, high-shouldered, deep-chested antelope with long legs, a short neck and a very long, narrow face. The horns are carried on hollow bases, or 'pedicels', and show considerable variation (450–830mm) from individual to individual and from region to region. Coloration also shows considerable regional variation (red and black in the Kalahari, tan in East Africa, golden-brown in West Africa) and also individual variation, especially in the Korkay from Ethiopia (*A. b. swaynei*) in which the overall body colour ranges from silvery purplish to red or dark brown, and the blotches of black on shoulders and knees vary in shape and extent. The Hartebeest has preorbital and pedal (hoof) glands.

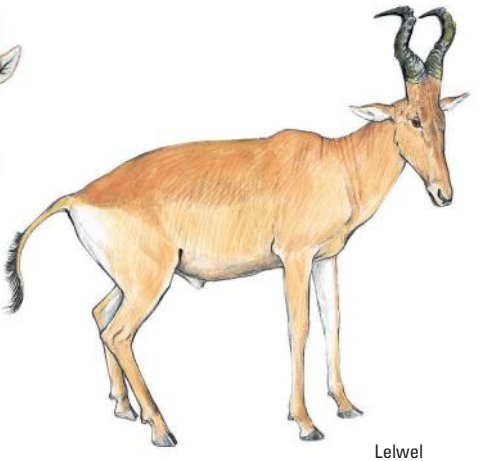
GEOGRAPHIC VARIATION **Bubal**, *A. b. buselaphus* (N Africa), extinct 1925; **Kanki** (Western Hartebeest), *A. b. major* (W Africa); **Lelwel**, *A. b. lelwel* (L. Chad to L. Turkana); **Korkay** (Swayne's Hartebeest), *A. b. swaynei* (Ethiopia); **Tora**, *A. b. tora* (E Sudan and N Ethiopia); **Kongoni** (Coke's Hartebeest), *A. b. cokii* (S Kenya and N Tanzania); **Nkonzi** (Lichtenstein's Hartebeest), *A. b. lichtensteinii* (central and SE Africa); **Khama** (Red Hartebeest), *A. b. caama* (Cape, Kalahari).



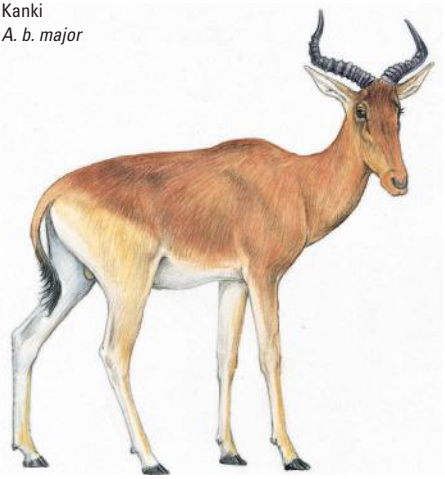
Korkay
A. b. swaynei



Kanki
A. b. major

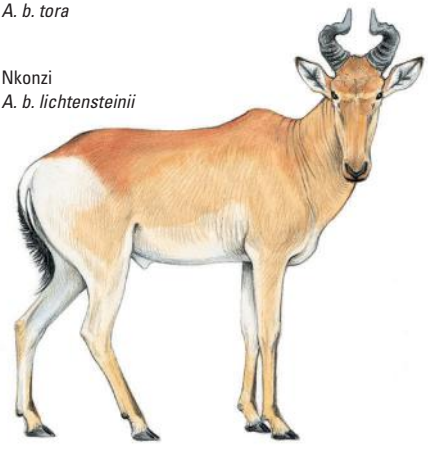


Lelwel
A. b. lelwel

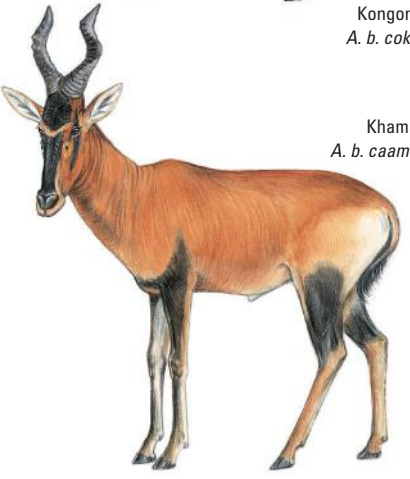


Tora
A. b. tora

Kongoni
A. b. cokii



Nkonzi
A. b. lichtensteinii



Khama
A. b. caama

The eight subspecies listed above have been generally recognised since 1894. Among some 50 named forms are many collected from interzones between the ranges of these eight subspecies. Most of these appear to be unstable hybrids rather than graduated intermediate forms, suggesting that former isolation has broken down as three forms, the Lelwel, Khama and Nkonzi, expanded their ranges.

DISTRIBUTION Formerly all African grasslands and savannas (except for a very narrow strip between the R. Juba and R. Tana and the South African Highveld). The short-pedicelled, more conservative subspecies (Tora, Korkay, Kongoni) live in NE Africa. The Khama in the Kalahari and Kanki in W Africa have high pedicels and are more advanced. The Lelwel, with the highest pedicels, appears to have intruded into the former ranges of all its neighbours, in each case creating hybrid zones. The Nkonzi, possibly derived from the same stock as the Kanki, has also colonised a vast territory wedged between the ranges of the Kongoni and Khama, apparently hybridising with both (how extensively remains to be determined).

HABITAT Although regional differences are substantial, Hartebeest are consistent everywhere in being grazers that live on boundaries between open grassy plains or glades and parkland, woodland or scrub (often on shallow slopes). They go to water regularly (but territorial males go without for quite long periods). They move down drainage lines for grass and water in the dry season and up onto better drained, thinly grassed woodlands during the rains.

FOOD Grazers, selective of neither species nor component parts of the grass. However, certain species are avoided, notably *Cynodon*, a grass that is readily grazed by other herbivores. All studies have shown that broad-leaf foliage accounts for less than 5% of the diet.

BEHAVIOUR Female Hartebeest are gregarious and to variable degrees move up and down shallow grassy valleys in pursuit of the best grass. Males become dispersed along the margins of each drainage line and establish dung-marked territories that embrace all the vegetation types from top to bottom of the slope. Where there is pressure from neighbours, territories may get narrowed but nearly always from the sides and not from above or below. Males waylay female groups as they pass through their territories. In some areas breeding is compressed into a short period during the rains (May in Uganda) and most males only become territorial at this time. In other areas some breeding continues throughout the year and territories are held more or less continuously. Males mark their territories with dung and posture with the head held upright and the legs placed well back. This is a gesture that suggests ritualised defecation and may serve to deter neighbouring males and attract passing females. Males fight most intensely in the presence of oestrous females and are especially aggressive towards attendant male offspring. At high densities males are sometimes killed in fights. Females defend their young vigorously and also form temporary all-female hierarchies in which threatening gestures with horns are noticeable. A single young is born after an 8-month gestation and growth rates are strongly influenced by nutrition. Sexual maturity is reached in 1 year in some populations and not until the fourth year in others. Animals live for up to 19 years.

ADAPTATIONS With the exception of the Nkonzi, *A. b. lichtensteinii* (which could be regarded as an incipient species), all subspecies have been recorded in very large dense herds at various times (the same was true of the Bubal in the 1830s and 1840s in Souf, Algeria).

Populations crash to very low levels during droughts, disease epidemics or under sustained competitive pressure from cattle. However, they recover quite rapidly when conditions improve. This capacity to build up their numbers is fuelled by subsistence on a normally super-abundant resource. They are also socially versatile, with females finding the best pastures at all density levels and the males adjusting the size and distribution of their territories accordingly.

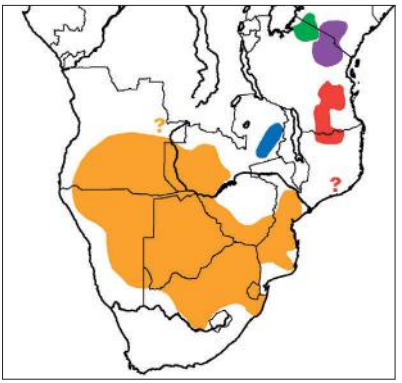
STATUS Extinction of the Bubal should serve as a warning about the vulnerability of this species. At present the Tora, Korkay and Kanki are all at very low levels. The Korkay is now extinct in Somalia, where it was once present in vast herds. Apart from being easy to hunt and possessing very tasty meat, this antelope declines wherever there is competition from intensive cattle-keeping. The Tora is listed as endangered (IUCN) and the Korkay as threatened. Other subspecies are not endangered at present but the pastures of all remaining populations are coveted by livestock interests.

BRINDLED GNU *Connochaetes taurinus*

OTHER NAMES Common Wildebeest. Fr. *Gnou bleu*. Ger. *Streifengnu*. Swah. *Nyumbu*.

MEASUREMENTS HB 1.7–2.4m. T 600–1,000m. Sh. ht 1.15–1.45m. W 140–260kg (♀), 165–290kg (♂).

RECOGNITION A dumpy, thick-necked, long-faced antelope with horns that flare out sideways and then upwards (rather like a cow's). The flat, rather square nasal plate (with hair-lined, flap-edged nostrils) is bounded by an even broader, grass-nibbling mouth. Dense tufts of hair on the long, convex muzzle conceal very active preorbital glands and help to diffuse scent from them. The muzzle is black in all subspecies, as is the shaggy mane and tail. The body colours of the four or five different subspecies varies from dark grey-brown to slate blue to pale greyish fawn, with variable degrees of brindling. This strongly textured streaking of the neck, shoulders and flanks mimics the visual effect of a long, lank mane very closely. The neck and chin are bearded in long, black, brown, cream or white hair. The short legs are brown or ochre, with pedal glands between the large true hooves (there are prominent false lateral hooves).



Brindled Gnu

GEOGRAPHIC VARIATION Brindled Gnu or Blue Wildebeest, *C. t. taurinus* (south of the R. Zambezi, Kalahari); Cookson's Wildebeest/Gnu, *C. t. cooksoni* (Luangwa valley); Johnston's or White-banded Wildebeest, or Nyassa Gnu, *C. t. johnstoni* (SE Africa); Eastern White-bearded Wildebeest/Gnu, *C. t. albojubatus* (S Kenya, NE Tanzania, east of the Rift Valley); Western White-bearded Wildebeest/Gnu, *C. t. mearnsi* (N Tanzania and S Kenya, west of L. Natron and L. Manyara).

DISTRIBUTION Open bushland and grassy plains in relatively dry areas of E, SE and south-central Africa. These animals, dependence on water limits their extension into drier regions but they persisted on the North African littoral into prehistoric and possibly historic times.

Brindled Gnu *C. t. taurinus*, male

Eastern White-bearded Wildebeest *C. t. albojubatus*

HABITAT Short grasslands (maintained by fire, shade, rainfall, water table, drainage, soil chemistry, herbivore grazing and trampling), always within about 20km of permanent water. Migration permits them to rotate pastures where these requirements are seasonal.
FOOD A wide variety of nutritious grasses that form short swards. At times Brindled Gnu may be forced to strip leaves from tall stems but this is a temporary and inefficient expedient. They are unable to graze persistent rank growth, which helps to explain their absence from many areas of equatorial Africa and their inability to survive (as reintroductions) into long-grass areas.
BEHAVIOUR They are social grazers that congregate in response to the local distribution of short grass pastures and water. Where these are adequate throughout the year, females and their young can remain permanently on home-ranges of a few hectares. Other similar female groups may share some of their range without friction but external intruders can be severely harassed. Where their food and water dry out, resident gnus tend to move on to more extensive seasonal pastures. Here they join other gnus, soon losing their local identities in the amalgam of herds. These seasonal aggregations are sometimes quite temporary.

Permanent large herds are more continuously nomadic, with females joining up to lead mass movement from one major pasture to another. The celebrated Serengeti migration is just such a circuit, in which the dry season is spent on the grasslands of the L. Victoria littoral and the rainy season on ashy volcanic plains closer to the Rift Valley. During this annual cycle females initiate movement off the open plains as surface water and herbage begins to dry out. Both sexes are in peak condition after several months on the fertile volcanic pastures.

As with Kob, Topi and many other mammals, enforced collectivisation triggers the hormonal changes in both sexes that are known as 'the rut'. Rutting males attempt to exclude each other from access to oestrous females. Because movement along the route is jerky (the mega-herd moving on after exhausting each pasture), males tend to win 'territories' that are simply marked out by their own behaviour. They 'broadcast' sound, scent and eye-catching visual displays in the form of belching grunts and snorts, flurries of scent (transferred from the face to everywhere they can reach) and frantic leaping, cavorting and head-shaking. Such territories can be no more than a fraction of a hectare. Depending on the pace of movement the male can remain in one place for many days or a few hours as herds continue their relentless movement. A scatter of males remains in the wake of the herds, exhausting their energies in fruitless posturings and stand-offs with a fast-diminishing audience of other left-over territorial males.

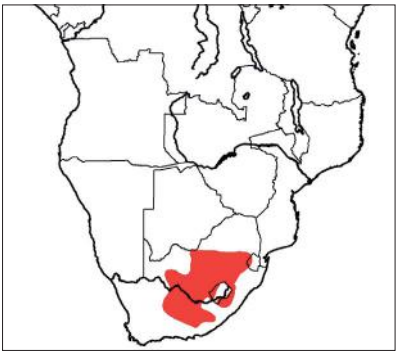
One calf is born to each female in the following wet season, 8 months later. While some large carnivores can keep up with or waylay the herds, one of the benefits of nomadism is outmarching the predators. Synchronised calving also helps to reduce the toll from predators. Births take place on exposed pastures, almost all in the space of a few weeks, and calves born outside this period seldom survive.

The newborn begins walking within minutes. It is tan at first but acquires the distinctive gnu colouring by stages, beginning within 1 or 2 months of birth. Rates of maturity vary, with females becoming fertile by about 16 months. Males do not normally take up territories until they are 4 or 5 years old. Brindled Gnu are known to live for up to 20 years.

ADAPTATIONS Isolated individuals and scattered small groups are seldom found very far from the annual range of a much larger regional population. Attrition is generally quite swift in such vulnerable outliers. Although they have stamina and a fast turn of speed, adults can be outrun and killed by at least six major carnivore species. Their calves are vulnerable to many more. Gnus are therefore adapted to living in large, dense herds. As grass ruminants, a large part of their body mass is given over to the digestive tract. Since their security depends more in belonging to a herd than in outrunning predators (as Hartebeest can do), gnus do not need such long legs, heads and necks. This is a special advantage for males because they can specialise in becoming efficient fighters and horn-wrestlers with their heavy necks, heads and horns. Females must also be sufficiently robust in order to defend their offspring from the males.
STATUS Land settlement, livestock and their diseases, fences and easy poaching with modern weapons all represent threats. More than most species, the Brindled Gnu is dependent on deliberate conservation policies for its survival because its year-round requirements of water and pasture must be met and each local population must remain sufficiently numerous to be viable. Each subspecies is well represented in conservation areas and national parks but both protection and land areas are often inadequate. They continue to decline and are unlikely to survive outside such areas. Overall, the Brindled Gnu is rated as not endangered (IUCN) but that status will be tested in future years.

WHITE-TAILED GNU *Connochaetes gnou*

OTHER NAMES Black Wildebeest. Fr. *Gnou à queue blanche*. Ger. *Weisschwanz Gnu*.
MEASUREMENTS HB 1.7–2.2m. T 0.8–1.0m. Sh. ht 0.9–1.21m. W 110–160kg (♀), 140–180kg (♂).
RECOGNITION A stocky, thick-coated antelope with heavily bossed horns that swing down, forward and upwards in tight angular hooks. The long muzzle is very broad, flat-fronted and covered in dense black fur. The flapped nostrils are set above a wide rectangular mouth. The body colour is dark brown, with a black beard and chest tassels. The upright mane hairs are off-white with intensely black tips. The long, flowing tail is wholly white.



White-tailed Gnu

The pelvis is peculiarly prominent. The large hooves of the forelegs have interdigital glands. Preorbital glands are also very active, especially in adult males (scenting not only the face but, by transfer, also the body and tail).
GEOGRAPHIC VARIATION None (there are four obsolete subspecies names).
DISTRIBUTION Originally migratory over a large part of the Karoo and Highveld. Overall range from the valley of the R. Vaal in the north to the R. Salt in the south, and from the Orange R. valley in the west to the Drakensberg Mts in the east. Now extinct as a wild animal.
HABITAT Temperate grasslands and Karoo shrublands where it migrated between summer pastures in the Karoo and eastwards to grasslands of the Highveld during the winter. These large-scale movements ceased when European settlement moved into the interior where, by the mid-19th century, this species had been brought close to extinction.
FOOD Grazes but supplements grasses with succulents and shrubs (such as *Pentzia*, *Salsola*, *Nenax* and *Osteospermum*), which permits grazing of the arid Karoo without regular water. It is more continuously active in cool weather but lies up for the heat of the day in summer.
BEHAVIOUR Unknown as a wild animal but some reconstruction has been possible on the basis of studies of small groups on fenced farms or reserves. Females wander in groups of up to 60 over home-ranges of about 100ha. As they pass through male territories they are inspected and the male attempts to deter them from passing on into the territory of his neighbours. This herding is most intense during the period of female oestrus. Because most females mate only at the end of the hot wet summer (March–April) it would appear that mating used to coincide with a massed eastward shift towards the Highveld winter pastures. Births more than 8 months later (250 days' gestation) would have been on their summer range in the Karoo. In confinement females form hierarchies and fight females not already known to them. By contrast, male bachelor groups generally show

White-tailed Gnu

few signs of aggression and some animals in the group have been observed to come to the rescue of bullied, bawling subordinates. This species has evolved particularly dangerous horns and, with them, elaborate appeasement gestures (including prostration). Yearling offspring are generally driven off by their mothers after the birth of a new calf. For the 6–9 months before weaning, mother and young remain very closely bonded. Young males do not normally take up territories until they are 4 years old, at which time they posture, fight challengers and mark the centre of their ranges with dung and urine in which the male paws and rolls. The thick coat is well suited to hold this scent (and that from the preorbital glands) and rutting males have a pervasive rank odour. They are also very vocal with a metallic snort, a two part '*ge-nu*' (hence the Khoi name) and a very resonant, single '*hick*' which is uttered with a violent spasm of the head and neck.

ADAPTATIONS The front-facing horns are extremely dangerous when hooked forwards and upwards from below. The animal's kneeling position while fighting greatly mitigates this danger while hefty bosses on the top of the head serve both as shields and battering rams during ritualised fights between rivals. However, in any normal frontal encounters with their environment (including other gnus) close contact is debarred not by spikes but by the rounded midshafts of the sharply angled horns. This barrier protects the muzzle and especially the preorbital glands from all such direct contacts. As a consequence White-tailed Gnus are unusual in hardly ever rubbing one another face to face, nor do they normally rub their face glands on the ground or vegetation. Instead, liquid secretion flows along hair tracts down into the beard and up into the bizarre tuft of long hair on the muzzle (found in both sexes). Beard and tuft therefore act as scent-dispensers as well as 'enlargers', extending, together with the mane and haired chest, the silhouette of the forequarters. In the intensely competitive context of migrating, mating herds, such characteristics would appear to have magnified the impression of physical power (further enhanced by dark colour which emphasises mass). Their cavorting, head-tossing and kicking would appear to exaggerate the energetics of movement while their amplified voices and behaviour such as rolling and pawing augment the social signals transmitted by strong scent. Their arched crests and long white tails served to make their large repertoire of displays highly conspicuous.

STATUS Private initiatives in the face of reluctant, indifferent or hostile policies have saved many species from extinction in South Africa, of which the White-tailed Gnu is one. Even now, many small farms are replacing livestock with indigenous herbivores. Vested interests in pastoral agriculture will probably not allow White-tailed Gnus sufficient space to begin behaving as wild animals again. Nevertheless, from a nadir estimated as low as 300–600 animals, present populations have risen to about 10,000 (however, inbreeding presents some problems). Currently rated as rare, but not endangered.

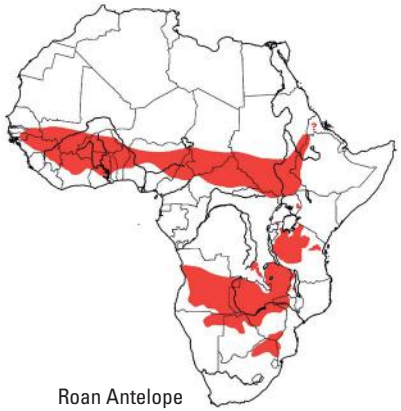
HORSE-LIKE ANTELOPES Hippotragini

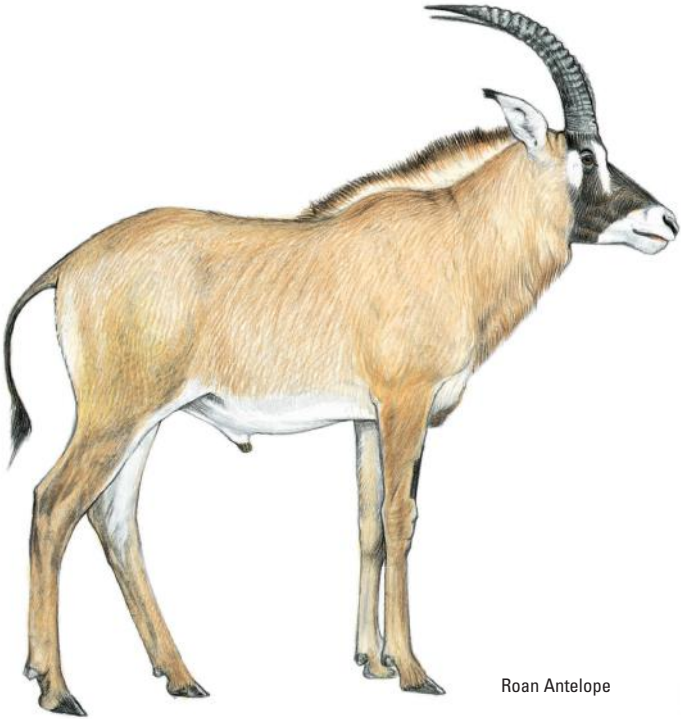
Roan and Sable Antelopes	*Hippotragus* (2 species)
Oryxes	*Oryx* (3 species)
Addax	*Addax nasomaculatus*

RECOGNITION Large, barrel-bodied antelopes with long, slender and well-annulated horns, long ears and broad, heavy hooves (with well-developed pedal glands). False hooves are particularly well developed in the oryxes and Addax. The coat is sleek, in various shades of tan, white and black, and the face is striped rather like a goat or gazelle. The thick, tapering necks and mane earned these antelopes their Latin name, Hippotragini, which means 'horse-goat'. Sexes are similar but males are heavier and have thicker horns. Some species have vestigial preorbital glands.
GENEALOGY Horse-like antelopes share a common ancestry with caprines. Like them, they are arid-adapted and represent an early, grass-eating 'giant' branch. Two 7 million-year-old fossils from the south-eastern Sahara are thought to represent basal hippotragines. By 4 or 5 mya oryxes (in more or less modern form) were already abundant in North Africa. The fact that no other bovid has been able to challenge them for the larger-scale desert niche implies that they have had a long head-start in adapting to heat, drought and unpredictable desert pastures. The Roan Antelope and Sable Antelope occupy isolated positions in the spectrum of tropical antelopes and the teeth of fossils confirm their common origins with oryxes, suggesting that they moved south from drier, more northern habitats.
GEOGRAPHY Although now exclusively African, there are fossils from India and Europe which suggest that the ancestral lineage of these antelopes was once more widespread.
ECOLOGY All species are grazers, with molar teeth well suited to grinding hard grasses (Roan Antelopes possess particularly broad teeth). They have specialised in exploiting zones with an impoverished fauna and flora. Much of their range corresponds with the 'Precambrian Shield' – extensive areas of low fertility and leguminous vegetation. Their narrowed choice (even within the tropics) is due to their attachment to particular localities in which they build up intimate knowledge of large home-ranges (that may include systematic avoidance of areas with numerous predators and competitors).
NATURAL HISTORY Anatomy, ecological dispersal patterns, modes of communication and social structures have probably been influenced by an ancestral 'desert ordeal.' Young animals are exceptionally social and active. They spend much time playing or rushing around, with stylised gaits, horning objects or mock-fighting.
ADAPTATIONS Horse-like antelopes are unusual in that the females have horns as long as those of the males. Female social units tend to have closed membership. Horns provide them with the means of excluding outsiders from scarce resources and resisting any attempt by males to limit their movement or threaten their offspring.

ROAN ANTELOPE *Hippotragus equinus*

OTHER NAMES Fr. *Rouanne, Hippotrague*. Ger. *Pferdeantilope*. Swah. *Korongo*.
MEASUREMENTS HB 1.9–2.4m. T 370–480mm. Sh. ht 1.26–1.45m. W 223–280kg (♀), 242–300kg (♂).
RECOGNITION A tall, powerful antelope with a thick neck, robust muzzle, long, droop-tipped ears, and massive, arched horns (500–1,000mm in males). The hooves are large (with pungent interdigital glands) and the false hooves are prominent. The coat is very coarse, becoming shaggy on the throat; hairs on the upright mane are dark-tipped. The face pattern varies individually but also regionally (the dark markings are more extensive in the north, the light ones in the south). Body colour is also subject to both individual and regional variation (from greyish in the south, more tawny in the north, to reddish in


Roan Antelope



Roan Antelope

the moister parts of its range). Tail lashes, earflips and the penis of the male are all made more conspicuous by dark tips.

GEOGRAPHIC VARIATION Two main populations, provisional subdivision as follows. Northern savannas: *H. equinus koba* (Senegal to Nigeria), *H. equinus bakeri* (Chad to Ethiopia): reddish in south, i.e. *charicus* type. Southern savannas: *H. equinus equinus* (southern Africa), *H. equinus langheldi* (East Africa), *H. equinus cottoni* (central Africa).

DISTRIBUTION Formerly very widespread in northern savannas and woodlands and in the more westerly parts of the southern savannas. Largely absent from the eastern seaboard and its hinterland. They once ranged from Sahelian steppe (but only within reach of water) and flat floodplains through various woodland and savanna types to montane and plateau grasslands up to 2,400m.

HABITAT Roan Antelope habitats are definable less by the exact composition of plants than by the scarcity of other herbivores. Even within very diverse communities of herbivores, Roans prefer localities in which there are few competitors and carnivores. In many areas they have distinct wet- and dry-season ranges, dispersing in the former and concentrating in the latter. Areas of a few square kilometres are grazed intensively for weeks or even months but overall ranges in South Africa have been estimated at 60–120km^2. In Tanzania a herd of 14 animals was seen to inhabit an area of 12km^2 over a period of 17 years. Roans prefer grasslands with few trees, park-like savannas and mosaics where there are clumps of trees or woodland margins in which shade and quiet resting places can easily be found. Although predators might be an ultimate factor deterring Roan Antelopes from certain areas, they are not entirely passive and have been seen to face-off and threaten approaching Lions and African Wild Dogs on a number of occasions.

FOOD Grazers of medium to short grasses belonging to dominant species, such as Red Oat Grass (*Themeda triandra*), thatch grass (*Hyparrhenia*) and couch grass (*Digitaria*). Roans occasionally browse shrubs or herbs and pick up *Acacia* pods in the dry season. They drink regularly.

BEHAVIOUR Herds totalling 5–35 animals (average about 10) are made up of females and their young attended by a single adult male who excludes other males. Such groups circulate through

a well-known and mainly exclusive home-range but may converge temporarily on a pasture that is shared with other Roans while grazing. Such aggregations are rare and both individuals within herds and separate herds maintain a distance between one another. When adult males meet they strut in 'proud' lateral circuits before bounding forward, dropping on their knees as they clash their horns violently together. Submission is signalled by lowered head, concealed tail and mute, open mouth. Extreme submission may lead to crouching flat on the ground. Young animals within a herd associate very closely (and are sometimes left on their own).

Breeding takes place throughout the year but births are rare in the dry season. The gestation period is about 280 days. Births take place in seclusion and the mother returns to the herd within a week. Once the young can keep up it also emerges from hiding and joins the herd. Young Roan are a focus of attention and attraction not only from the mother but also from all other immature animals. Suckling lasts 4–6 months. Sexual maturity is reached by 2 years in females while males are expelled from their maternal group at about 3 years, spending the next 3 years in a peripheral 'bachelor' group (of up to ten young males) before winning an apparently permanent or semi-permanent association with a female herd. Roans are known to live for up to 17 years.

ADAPTATIONS The Roan Antelope derives from a giant species that is widespread in East and southern African fossil deposits. Although latterly both existed contemporaneously, the giant form has a longer history (going back at least 2 million years). The Roan's behaviour and ecological niche (e.g. a slow gait of less than 60kph, water dependence and occupation of extensive home-ranges) may be conservative characteristics appropriate to very large antelopes.

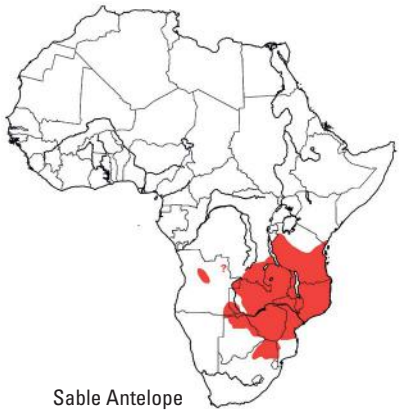
STATUS In spite of their extensive distribution, Roan Antelopes have seen a substantial contraction in range and numbers during the past century. The main threat has come from ever expanding livestock usurping their water and pasture. Their close attachment to localities and routines is linked with a very poor ability to colonise or recolonise. Their absence down the eastern littoral could be due to past depredations of disease and/or large human populations (before historic records). Although Roans are close to extinction in Mauritania, Niger, Uganda, Rwanda and Kenya, their overall status is not yet endangered (IUCN).

SABLE ANTELOPE *Hippotragus niger*

OTHER NAMES Fr. *Hippotrague noir*.
Ger. *Rappervantilope*. Swah. *Mbarapi, Palahala*.

MEASUREMENTS HB 1.90–2.55m. T 400–750m.
Sh. ht 1.17–1.43m. W 190–230kg (♀), 200–270kg (♂).

RECOGNITION A large, strongly built antelope with a thick neck, long, narrow muzzle, pointed ears, vestigial face glands, large, compact hooves and a longish, tufted tail. The Sable Antelope is celebrated for its magnificent, arched horns, which commonly exceed 1m in length and reach over 1.6m in the Angolan Giant Sable. The upright mane reaches to behind the shoulders. The coat is short and glossy in the tropics but grows longer in the south (and during the winter in captivity). Infants are dun-coloured and almost without markings. Older juveniles and young adults are rich russet, with white-striped muzzle and ears, belly and inner surfaces of the hindlegs. As males mature black tints on the face, flanks and shoulders begin to suffuse the red until, by 5 years (but for the white face pattern and underparts), they are black. Females of the southernmost population also turn black. In other populations females blacken more slowly and less completely.


Sable Antelope

GEOGRAPHIC VARIATION Southern or Black Sable, *H. n. niger* (south of the R. Zambezi); Miombo or Common Sable, *H. n. kirkii* (R. Zambezi to W Tanzania); Zanj Sable, *H. n. roosevelti* (East African littoral, north of R. Zambezi); Giant Sable, *H. n. variani* (Angolan).

DISTRIBUTION Scattered through the central and eastern parts of the miombo (*Brachystegia*) woodlands, with an isolated population in Angola.

HABITAT Miombo (*Brachystegia*) woodland. In fact they are not wholly confined to the woods, living there from about October–May and shifting out as these well-drained and seasonally burnt

Sable Antelope

woodlands begin to dry out. They gather closer to permanent water, in valley-bottom grasslands, or mbugas, for the dry season. Here they have firm ground under foot and can exploit seasonal grassy mosaics (many created by local fires) but still remain close to the woodland–grassland edges. Such shifts may involve a few kilometres in richer more dissected landscapes or a wholesale seasonal shift in more impoverished ones. Estimates of the extent of home-ranges exceed 300km^2 in the latter situation and only 10–25km^2 in the former.

FOOD New grass growth or grasses of medium height belonging to locally dominant types are preferred. Well before the rains begin Sable Antelopes leave the valley bottoms (like horses they avoid deep mud if they can) and greatly increase the normally small proportion of woody foliage in their diet. Arrival of the rains and regrowth of the thin woodland grasses follow the temporary flush of leaves. This is a time of maximum dispersal in which small groups constantly rotate their pastures.

BEHAVIOUR Females form regional 'clans' of fewer than 100 animals that readily divide up into subgroups of unstable membership. The fission of these subgroups (about 10–30 animals) may range from a few hours up to a month or more. Longer periods apart eventually lead to the formation of separate clans. In spite of overlaps in their home-ranges, females from different clans are hostile to one another when they meet. Adult males sometimes follow these herds during their movements (a pattern typical of Roan Antelopes and oryxes) but the majority disperse themselves over the available pastures and control territories with boundaries that tend to coincide with rivers, forest margins, banks (or even roads). Here the males makes very vigorous attempts to detain any herd that passes through, persistently and very fiercely driving them back towards the centre of each territory. During the period they are kept there all adult females are inspected and oestrous females are mounted. Copulation is achieved in a matter of seconds, with a sudden bipedal lunge after long-

drawn-out preliminaries, including much chasing, testing, nudging and kicking. Breeding peaks occur but seem to have more to do with poorly understood social dynamics than with seasons. Gestation lasts 240–280 days. The sandy-coloured calf stays concealed for some 3 weeks and then joins the other youngsters in the mother's group. It only seeks out its mother for milk but will call her with a high, piping call when lost. Males are driven out into 'bachelor' groups at about 3 years, joining 2–20 other young males. Females usually have their first calf after they reach 3 years old. Sables are known to live for 17 years.

ADAPTATIONS Sable Antelopes are secondarily territorial. One indication of their nomadic, open-country origins is the male's reliance on visual self-advertisement. Unlike other woodland and forest antelopes scent-marks are subordinate to the male Sable's posturings and direct herding of the females. Black colouring is both the mark of super-seniority in the colour-coded hierarchy of the female herd and also the central beacon of a defended territory. Battered bushes, dung piles and foot-scrapes in the centre of a 3 or 4km^2 territory may help deter other males but it is the imposition of male physical presence that dominates both hierarchy and territory.

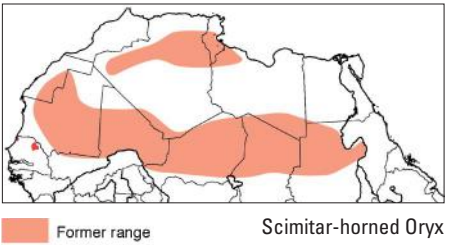
STATUS The Giant Sable is rated as vulnerable. The Shimba population is rated as endangered and in South Africa it is rated as rare (IUCN). Elsewhere expansion of the livestock industry is forcing Sables into steep decline but they are not endangered (yet).

SCIMITAR-HORNED ORYX

Oryx dammah

OTHER NAMES Scimitar Oryx. Fr. *Oryx algazelle*. Ger. *Sabelantilope*.

MEASUREMENTS HB 1.90–2.20m. T 450–60mm. Sh. ht 1.10–1.25m. W 135–140kg.



Scimitar-horned Oryx

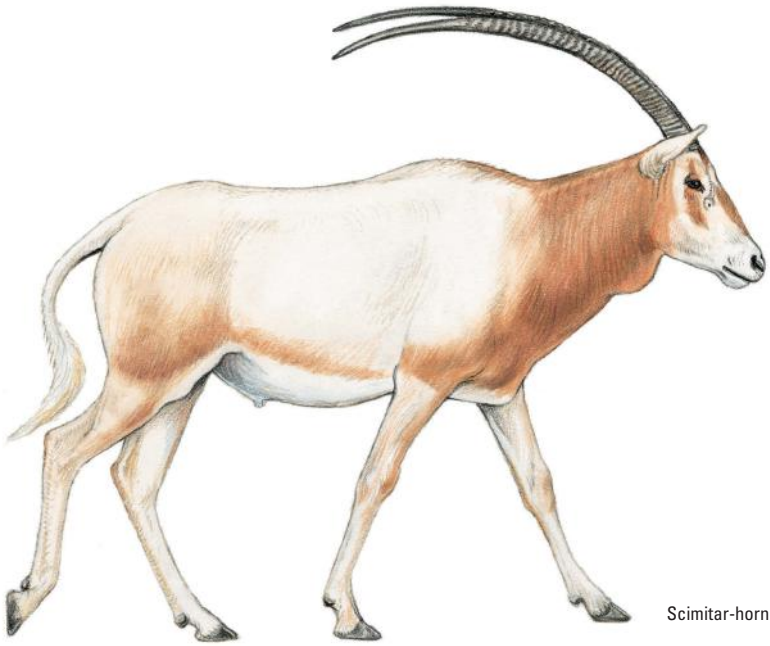
RECOGNITION A large, rotund antelope with a deep chest and relatively short, sturdy legs with broad hooves and prominent false hooves. The face is long with medium-sized ears and, unlike other oryxes, it has vestigial preorbital glands. Its horns are very long, slender and arched (1.00–1.15m), with many fine annulations. The tail is long and bushy. The vestiges of a structured pattern show up as pale apricot-brown tints on a predominantly white animal. Faint facial stripes run down the nose, cheeks and 'through' the eyes. The flanks and rump are also faintly striped or tinted while neck and shoulders look as though they are deeply stained with rust.

DISTRIBUTION Formerly from Morocco to Egypt and from Mauritania to Sudan along the interface between true desert and less arid Sahelian or Mediterranean habitats under an annual rainfall of between 75 and 150mm. Having originally ranged over more than 4 million km^2 it is now extinct in the wild.

HABITAT Semi-desert grasslands of the Sahel and their N Saharan equivalent. *Acacia*, *Commiphora* and Heglig (*Balanites*) growing in moisture-retaining troughs between dunes and outcroppings provided some woody cover and thin shade but it was flushes of grass that drew the nomadic oryxes back and forth across unknown distances. How far they travelled in order to take advantage of desert flushes was indicated by a single aggregation of 10,000 animals seen in Chad in 1936. An authoritative estimate of typical density suggests one oryx for every 40km^2 of desert habitat. At such a density the reservoir for this gathering was 400,000km^2, with the most distant animals coming in from about 300km away. This suggests that the potential range of an oryx group under every extremity might be in the order of 100,000km^2. The implications for their ability to orient as well as their stamina in a waterless desert are obvious.

FOOD Mostly grasses but herbs, shrubs, pods and fruits have been reported.

BEHAVIOUR The Scimitar-horned Oryx was nearly always seen in herds of 10 or more and it was capable of aggregating and dispersing in response to its very ephemeral pastures. Its reluctance to remain solitary was evident in the observed attachment of old males to parties of Dama Gazelles. While known to be opportunistic breeders, the oryxes were reported to have extended birth peaks around March and October. With a gestation of 242–256 days matings would have peaked at the end of winter and during the first rains. Birthing mothers sought a brief seclusion but both mother and baby rejoined the group within hours (some indication of the imperative to keep mobile at all times). Captive animals have lived for 17 years.

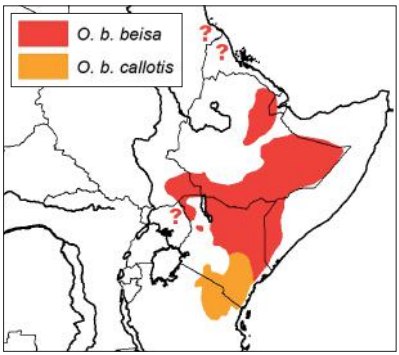


Scimitar-horned Oryx

ADAPTATIONS The almost white colouring of the Scimitar-horned Oryx is highly visible from a great distance. If its behaviour resembles that of the even whiter Arabian Oryx, then this colouring can be assumed to have helped 'lost' individuals to regain contact with the group. By standing on the top of a dune an individual would be able to see and be seen by other oryxes from a long way off. **STATUS** One aspect in the decline of this species is the fact that it presents an easy standing target. However, given that the N Saharan populations became extinct hundreds of years ago, it seems likely that its decline may also have ecological causes. The most obvious is disruption and competition from expanding populations of domestic stock. It is now extinct in all Saharan nations but has been reintroduced to fenced parks in Tunisia, Senegal and Morocco. Conservation remains a low priority for all Saharan nations. This species was rated as critically endangered (IUCN) but is now extinct in the wild.

BEISA ORYX *Oryx beisa*

OTHER NAMES Fringe-eared Oryx. Fr. *Oryx beisa*. Ger. *Beisa spiessbock*. Swah. *Choroa, Bara bara*. **MEASUREMENTS** HB 1.53–1.70m. T 450–500mm. Sh. ht 1.1–1.2m. W 116–188kg (♀), 167–209kg (♂). **RECOGNITION** A large, compact, muscular antelope with a thick neck, long face, long straight horns and distinctively shaped and patterned ears. The longish tail terminates in a black brush. Strong but slender legs terminate in large, very black hooves (and false hooves that are given extra visual emphasis by emerging from black tufts of hair). The brownish-grey coat is demarcated from black-and-white facial, flank and foreleg patterns. The line of the back-swept straight horns (600–1,100mm) continues right across the face in the form of a black stripe. Superficially there is very little difference between males and females.

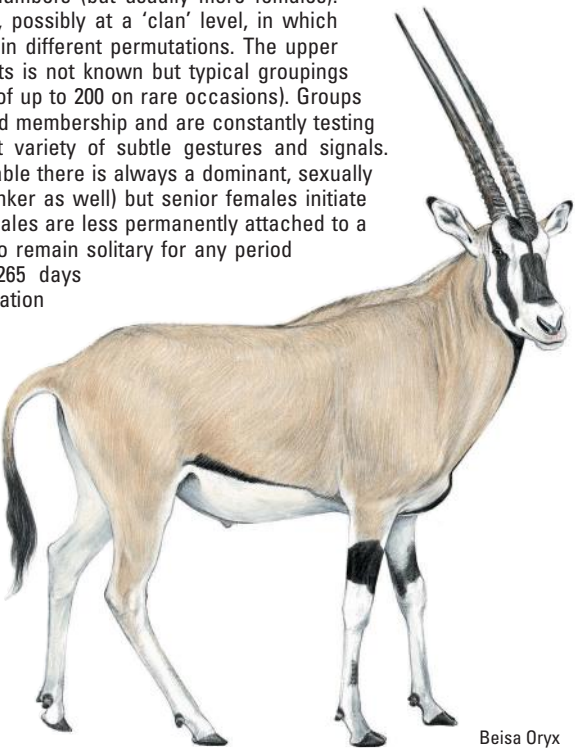


Beisa Oryx

GEOGRAPHIC VARIATION Beisa Oryx, o. *b. beisa* (north of the R. Tana); Fringe-eared Oryx, *O. b. callotis* (south of R. Tana).
DISTRIBUTION The Horn of Africa from the Red Sea littoral (Haddendowa) to Somalia and south to arid central Tanzania. Their most westerly limit is Jebel Lafon in South Sudan and Karamoja in NE Uganda. Some parts of their range have up to 250mm annual rainfall, more humid than for any other oryx. The Southern Oryx, or Gemsbok, of the Kalahari is a close relative, often classed as the same species.
HABITAT These oryxes inhabit arid grasslands and bushland but avoid tall grass in the rains (and thick bush in the dry season). Both grazing and the condition of the ground underfoot influence seasonal movements. They move out of waterlogged or soft-soiled depressions during the rains up onto higher ground but may return in regular cycles of movement. In the driest parts of their range movement is less regular and large numbers gather or disperse unpredictably. Densities vary greatly, with up to 1.4 per km^2 in the choicest localities. Home ranges of 200–300km^2 have been recorded for females and 150–200km^2 for adult males.
FOOD Grasses, but will browse *Acacia* and other shrubs in the absence of grass, especially during the dry season. During droughts they dig out tubers and roots with their hooves for moisture. Where water is available they drink regularly but can do without, having a lower rate of water turnover than a camel.

Beisa Oryx in subordinate head-low posture.

BEHAVIOUR Mixed herds are formed in which the sexes are sometimes equally balanced in numbers (but usually more females). Both sexes establish hierarchies, possibly at a 'clan' level, in which subunits can join up or disperse in different permutations. The upper limit of such local population units is not known but typical groupings can reach 60 (with aggregations of up to 200 on rare occasions). Groups probably have more or less closed membership and are constantly testing or asserting status with a great variety of subtle gestures and signals. Where herds remain relatively stable there is always a dominant, sexually active male (usually a second-ranker as well) but senior females initiate and lead movement. As a class males are less permanently attached to a group and are the only animals to remain solitary for any period of time. Of several estimates, 265 days appears the most likely gestation period. Breeding is not normally seasonal but occasional crops of synchronised births have been reported. Calves lie up for very variable periods (between 2 and 6 weeks). They join other young to form peer groups and may stay together up to a year. They become fertile by 18–24 months and have survived for 22 years in captivity.
ADAPTATIONS Beisa Oryxes indulge in ritualised 'tournaments' the function of which appears to be the testing and reinforcement of rank order.



Beisa Oryx

Black-and-white signals of Beisa Oryx flagged during a tournament display.

Commonly seen at dawn or during a shower these start with one or more animals running in broad circles. A galloping spurt builds up the momentum to permit a long, high-stepping, 'floating' pace in which the neck is bunched, chin raised and the head swung from side to side in rhythm with the pace. The black-and-white head flashes in time with the high-stepping knees and flying hooves. Because the most frequent and active participants are juvenile or young animals, this performance may be a primary way of learning and exploring social position. It is also possible that there is a spatial dimension and that the runner is learning to 'take a fix' that reinforces its memory of the home-range.

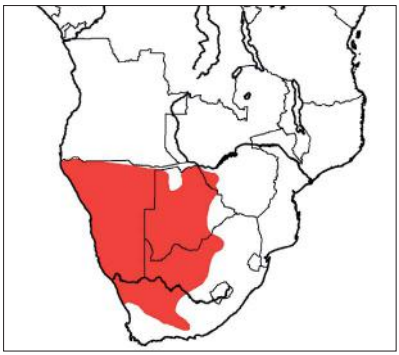
STATUS This species is known to have declined, especially in its marginal ranges in Sudan, Uganda, Tanzania and most especially in Somalia and Uganda, where its formerly extensive range is reduced to fragments and it is in imminent danger of extinction. Its range is being progressively usurped by livestock. Elsewhere it is in decline but not yet endangered.

SOUTHERN ORYX *Oryx gazella*

OTHER NAMES Gemsbok. Fr. *Gemsbok*. Ger. *Südafrikanischer Spiessbock*.

MEASUREMENTS HB 1.80–1.95m. T 400–470mm. Sh. ht 1.17–1.38m. W 180–225kg (♀), 180–240kg (♂).

RECOGNITION A large, very thick-necked antelope with long, straight horns (600–1,200mm) aligned with the muzzle, large, rounded ears and a long, bushy black tail. White muzzle, face-stripes, belly and 'stockings' contrast in every instance with bold black markings on the face, flanks, upper legs, midline and rump. Like other oryxes, the neck and shoulders are enveloped in exceptionally thick, inelastic and dense skin. This gives adult bulls a rather 'jacketed' appearance.

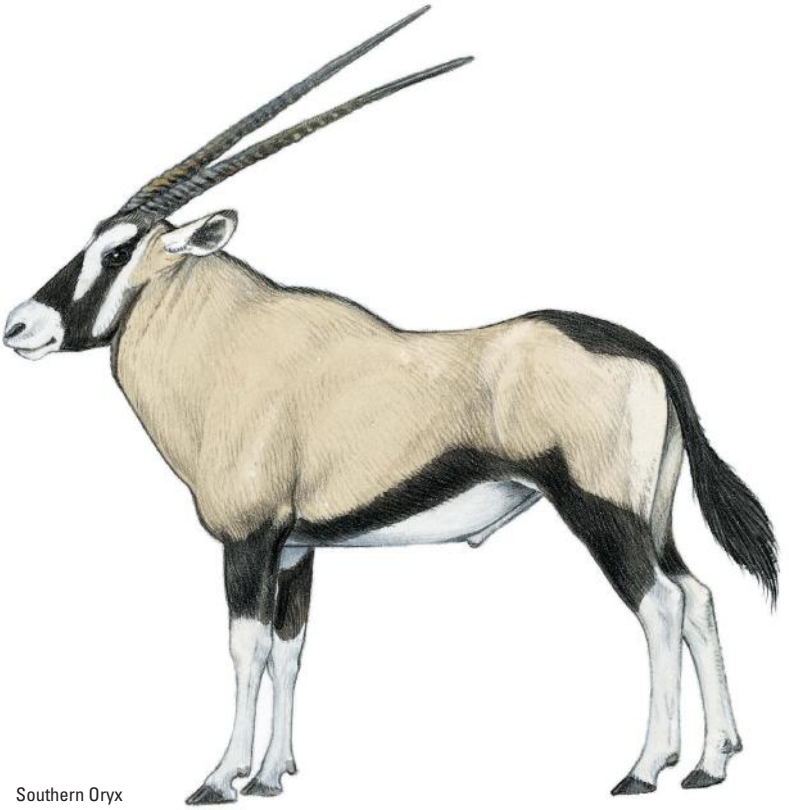


Southern Oryx

GEOGRAPHIC VARIATION Nine subspecies, none valid, but Angolan animals have narrower black markings.

DISTRIBUTION A Kalahari desert species that formerly ranged from the Karoo to near Benguela and from the Atlantic littoral to the upper Zambezi valley and W Transvaal. Exterminated from most of its South African range. It lives under an annual rainfall of 50–250mm.

HABITAT Wooded grasslands and *Acacia* bush of the central Kalahari and Karoo shrublands, entering wetter grasslands and bush along the margins of its main range. Its extensive distribution includes areas of very variable fertility and rainfall, with pastures permanent in some places, ephemeral in others. As a result, home-ranges vary from about 4km^2 to 400km^2. Female ranges, shared with other travelling companions, are always much larger than those of single males, which may centre on a particular locality for a long period. Animals are known to follow regular circuits between favourite localities where they may spend many weeks on small pastures. Their presence in such places may be marked by regularly used 'scoops' (for resting or ruminating in), pathways and neat little piles of excreta carefully placed by squatting males on bare pans or prominences.



Southern Oryx

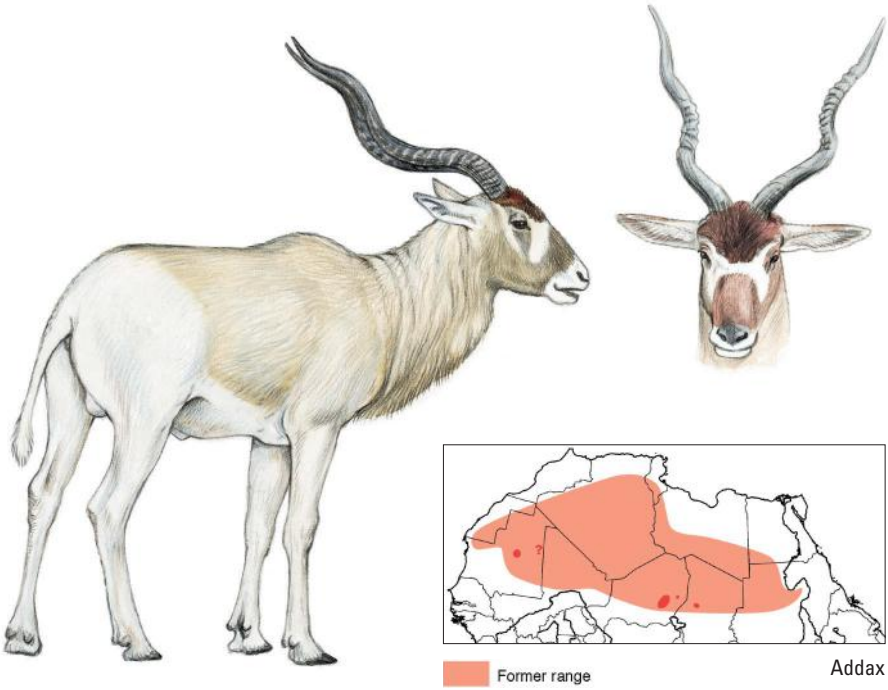
Seasonal and regional differences in the quality of their range are reflected in thick fat deposits under the skin and visible changes in their physical condition.

FOOD A grazer that will turn to browse or herbs in the absence of grass. It digs up tubers and roots for moisture and, in spite of being able to go without water, will go on long treks in order to find it and will dig deeply in dry riverbeds. Males will fight for access to water as well as to females. It regularly visits salt-licks.

BEHAVIOUR Although most female groups are nomadic and many males remain attached or in attendance, other, mostly old, males become much more sedentary. In Etosha NP, where year-round grass-growth can support them, a scatter of resident males may be less than 1km apart (behaving rather like Sable Antelopes in taking an interest in passing females). Female groups number up to 50 but occasionally aggregations of 400 or so have been seen. Breeding is not seasonal and one young is born after a 264-day gestation. Hiding places change frequently but newborn young remain concealed for 3–6 weeks. Animals mature at about 2 years and young males may remain in their mother's group for at least a year. They live for about 20 years.

ADAPTATIONS An observer with experience of all oryx species has noted that low-level aggressive behaviour is more sustained and continuous in this species than in other oryx populations. Such interactions involve threat displays, horn gestures, butting, circling and parallel-walking as well as outright fighting. Corresponding appeasement gestures are equally common; head-bowing, chin-lifting, head-throwing and bent-leg creeping are all directed at dominant individuals. Its very strong markings may enhance the semaphore of the Southern Oryx's intense social life.

STATUS In spite of great contraction of range, the Southern Oryx is well represented in major national parks as well as being tolerated in some of the large enclosures that now subdivide its former range. It is not endangered.



Addax

ADDAX *Addax nasomaculatus*

OTHER NAMES Fr. *Addax*. Ger. *Mendesantilope*.
MEASUREMENTS HB 1.20–1.75m. T 270–350mm. Sh. ht 0.95–1.15m. W 60–90kg (♀), 100–135kg (♂).
RECOGNITION A stocky, almost white antelope with long, annulated horns following loose spirals. The blunt, narrow head has a chocolate-brown tuft on the forehead, a paler-brown muzzle and eye-patches, a white face-mask, narrow ears and a short brownish fringe of hair down the throat. The broad, spatulate hooves have protruding false hooves and interdigital glands. Sexes differ very little in size and morphology.
DISTRIBUTION Formerly from the Atlantic to the Nile in the central Saharan desert; now extinct except for vestigial pockets in Niger, Chad and Mauritania, and possibly in Mali. Migrations in pursuit of seasonal flushes once brought Addaxes together in herds in excess of 1,000 animals.
HABITAT Sand-dune deserts (erg) and, formerly, clay-gravel plains (reg) and stony plateaus (hammada). The Addax is principally active at night and at dawn and dusk, resting up during the heat of the day.
FOOD Coarse desert grasses, but with distinct seasonal preferences. *Stipagrostis vulnerans*, *Panicum*, *Tribulus* and Drinn (*Aristida pungens*) were known staples. When grasses were absent the Addax browsed *Acacia* foliage and leguminous herbs, such as *Indigofera*. It was able to extract moisture from its food plants so effectively that one of the incentives for Saharan nomads to kill the Addax was to extract the copious water in its rumen.
BEHAVIOUR Formerly the Addax tended to travel in groups of 2–20 animals, sometimes aggregating in larger groups, very occasionally in hordes of many hundreds. Its movements within the Sahara tended to be longitudinal (oryxes reputedly made more latitudinal shifts). Groups were usually mixed but males would leave small piles of pellets (like oryxes) while females scattered their dung. Two birth peaks (autumn and late winter) were reported, suggesting that mating took place 8 months earlier during the coldest and hottest months of the year (but in each case at a time when there might have been movement and aggregations). Females mature at 18 months, males before they are 3 years old. Captive animals have lived for 19 years.
STATUS It is some measure of human penetration of the Sahara that this animal has been exterminated from a range of some 8 million km^2. At about the turn of the 20th century, in Ouargla

(the main Algerian city beside the great Eastern Sand Desert), fresh Addax meat was sold every week in the market. In less than a century, mounted or motorised hunters with modern firearms, together with expanding pastoral agriculture, have wiped out a species that has survived the vicissitudes of a desert environment for several million years. Critically endangered in Mauritania, Niger and Chad; extinct elsewhere.

SHEEP AND GOATS Caprini

Barbary Sheep	*Ammotragus lervia*
Nubian Ibex	*Capra ibex*
Walia Ibex	*Capra walie*

Mostly medium-sized, thick-legged, compact antelopes with limbs and hooves modified for climbing and leaping over rough or stony ground. Both sexes are horned but males have enormous arched or spiral horns. Scent glands are well developed and vary in site from species to species. All three African species have them between their hooves and on the underside of the tail.

As a distinctive Eurasian offshoot of the mainly African antelopes, the caprines may have diverged some 18 mya (while still resembling gazelles). In dentition and diet they have mostly remained adaptable and generalised but they have a modified physiology, limbs and social behaviour in order to cope with extreme climates and difficult terrain. Sheep and goats are thought to have split about 6 mya (the Barbary Sheep's closest affinity is with the Arabian Tahr, *Arabitragus jayakari*). A 1.5 million-year-old Ethiopian fossil, *Bouria anngettyae*, resembles an intermediate form, and late Pleistocene fossils of Barbary Sheep are numerous across northern Africa. By contrast, the ibex is an advanced type of goat and a more recent coloniser of Africa.

Evolving in Eurasia, caprines were restricted by the prior occupation of most richer habitats by deer. Their own exclusion of deer from extreme habitats in mountains may have derived from an early superiority under extremes of temperature and from their agility on broken ground. The N African mountains are a minor extension of the great mountain chains of Eurasia in which goat-antelopes evolved. Here they exploit unstable, seasonally variable pastures in relatively inaccessible terrain.

Within their restricted fastnesses, caprines are the most successful herbivores. Reaching high densities (especially in Asia), intense competition for mates among males has led to the evolution of very large horns in all the more advanced forms. Less specialised, small-horned species live in tropical Asian forests. Domestic species derive from non-African populations.

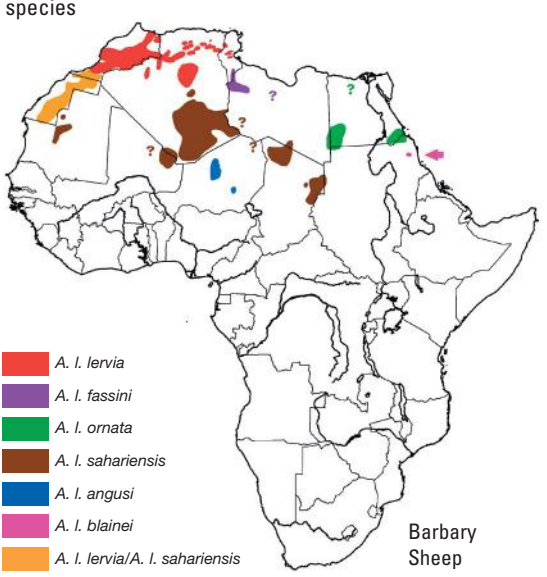
BARBARY SHEEP

Ammotragus lervia

OTHER NAMES Aoudad. Arui. Fr. *Mouflon à manchettes*. Ger. *Mähnenschaf*.

MEASUREMENTS HB 1.30–1.65m. T 150–250mm. Sh. ht 750–900mm (♀); 0.90–1.0m (♂). W 40–55kg (♀), 100–140kg (♂).

RECOGNITION A heavily built, thick, short-legged animal that is intermediate between a sheep and a goat. It has outward-arching horns which are slender and rounded in females, thick, ridged and much longer in males (which have twice the body weight of females). The face is long and tapered, ears small and the white mouth-parts contrast



Barbary Sheep

Barbary Sheep, male (*left*) and female (*below*)

with the pale tawny-brown coat colour. The fleece is woolly in winter, with a harsh texture, but moults to a sleek summer coat. Both sexes have tufts of hair on the upper foreleg and a hanging fringe down the throat but those of the males are denser and longer (almost reaching the ground). The short tail, naked below, like a goat's, has scent glands that are especially well developed in the male.

GEOGRAPHIC VARIATION *A. l. lervia* (Morocco to Tunisia), *A. l. fasini* (Hamra plateau, NW Libya), *A. l. ornata* (Egypt east of the Nile, and formerly in the Western Desert), *A. l. sahariensis* (Mauritania, Mali, C and S Algeria, and N Chad), *A. l. angusi* (Aïr Massif and Termit Massif, Niger), *A. l. blainei* (E Sudan).

DISTRIBUTION Sahara massifs and plateaus, originally from central Mauritania to the Hamra plateau in Libya and from the Algeria/Niger border area to Darfur in W Sudan. An isolated population occupied the Red Sea hills in Egypt and was reputed to have once ranged through Sinai.

HABITAT Desert hills and mountains, stony plateaus (hammada) and the slopes of valleys (wadis) well away from mountains. They avoid the sand deserts (ergs), which seem to have acted as barriers between regional populations. They prefer habitats with a choice of shady day-time retreats, either caves, rock overhangs or under trees, but at night will graze plains that are at some distance from any cover.

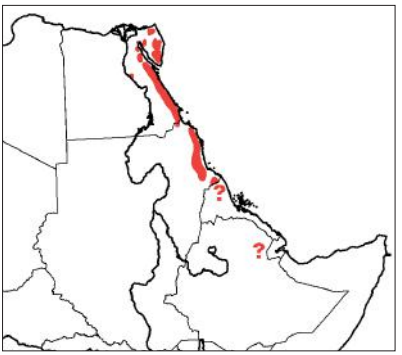
FOOD Grass and herbs; also browse shrubs and trees and will even get up onto their hindlegs in order to reach foliage. Barbary Sheep prefer to feed at dusk, dawn and during the night. They will drink water but can go without, extracting it from plants that become temporarily moister or are dewed at night.

BEHAVIOUR Barbary Sheep form small family parties in which a single adult male attends several females and their offspring. These tend to remain scattered but have been reported to gather into larger parties (i.e. 30 members) late in the dry season (July). A rut is thought to take place after the autumn rains (October) and births follow a gestation of 150–165 days. One or two young are born in a secluded site where mother and young lie up for a few days before rejoining their group. Females mature in about 18 months and captive specimens have been known to live for 24 years.

ADAPTATIONS Magnificent tassels on the forequarters of males are part of their intimidatory displays when competing for access to females.

STATUS It has taken centuries of expanding settlement and uncontrolled hunting to eliminate Barbary Sheep from most of their North African range. Competition and disturbance from livestock are probably the major causes of decline but hunting (with dogs and rifles) may have tipped the balance in some areas. Their meat has been reported to be a routine commodity on market stalls in Algerian and Moroccan towns and villages for nearly 100 years. In recent times military and oil-field personnel have used helicopters to reach their more remote haunts. The Barbary Sheep is now doing well on many ranches and reserves in the southern USA. In Africa it is vulnerable over all parts of its range.

NUBIAN IBEX *Capra nubiana*



Nubian Ibex

OTHER NAMES Fr. *Bouquetin de Nubie*. Ger. *Nubischer Steinbock*.

MEASUREMENTS HB 92–160cm. T 6.5–17cm. Sh. ht 65–110cm (♀), 0.75–1.1m (♂). W 50–125kg. Note: Nubian Ibexes average 80mm shorter and about 22kg lighter than Walia Ibexes.

RECOGNITION Close relatives of the domestic goat, ibexes have gone furthest in developing short, muscular limbs and chunky, rubbery hooves. Of all goats, male ibexes have developed the longest and most heavily reinforced horns (1.0–1.19m). They have short ears, a beard on the chin and a mane from nape to tail. The tail is short and secretes scent from glands on its lower surface. There are vestigial stripes on the face, flanks and thighs. The underside and inner limbs are white or cream, with white hock and knee patches. The Nubian Ibex is various shades of slaty brown.

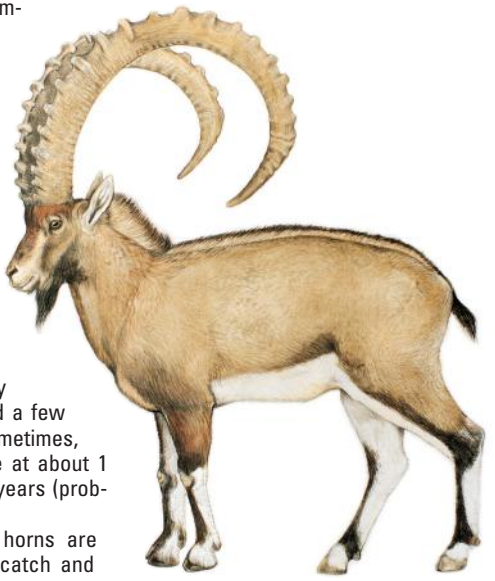
GEOGRAPHIC VARIATION Ibexes comprise a mainly Eurasian superspecies with various forms in Europe and the Middle East. Nubian Ibex and Walia Ibix are now considered to be separate monotypic species but were previously united in *C. ibex*.

DISTRIBUTION The Nubian Ibex formerly ranged throughout the more hilly parts of Arabia, the Middle East and NE Africa, but today, in Africa, exists mainly as isolated populations in the Red Sea littoral hills of Egypt and Sudan, from Suez to Massawa. There are no recent records from Eritrea.

HABITAT Rocky mountains, gorges, outcrops and loose stony screes in areas with a sparse cover of trees, scrub and grass.

FOOD Grass is grazed but main food plants are herbs, shrubs and trees. Leaves, buds, fruits and, in some cases, bark and flowers are eaten from a wide range of desert and montane plants. A special liking for the foliage of *Cadaba* and *Pluchea* has been noted.

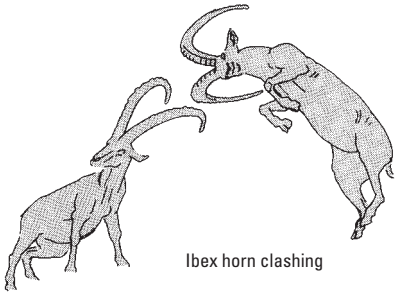
BEHAVIOUR Nubian Ibex live in confined ranges of a few km², or less. Females may be briefly on their own to give birth but normally have a loose association with other well-known females sharing the home-range. Females defend their young and fight strange male ibexes. Males lead an independent existence until the rut (between September and November) when dominant males seek to exclude all other males from oestrous females. At this time they eat little, fight and chase much, and suffer a marked deterioration in condition. Courtship involves a crouching approach, tongue-flicking, much wagging of the scented tail, urine-squirting onto chest and chin (the main function of the beard being scent-dispensing). The male also hisses, grunts and kicks; the combined impact of a barrage of sounds, scents and touches may both speed up oestrus and improve the female's receptivity. After a gestation of 150–165 days one, occasionally two, kids are born. They remain concealed a few days before joining their mother (also, sometimes, siblings of up to 3 years). Sexually mature at about 1 year; they are thought to live for about 12 years (probably more).



ADAPTATIONS The huge, knobbly, arched horns are designed to batter rivals in fights and to catch and

absorb the blows of opponents. Contestants vie for more elevated points from which to leap up and accelerate down onto the defender. These contests begin from standing positions no more than a couple of metres apart but they generate enormous forces and must give each fighter an accurate, if sometimes stunning, measure of his opponent's strength.

STATUS The species as a whole is rated by IUCN as vulnerable, but populations in Egypt and Sudan should be considered as endangered. Competition with livestock and hunting are the major threats.



Ibex horn clashing

WALIA IBEX *Capra walie*

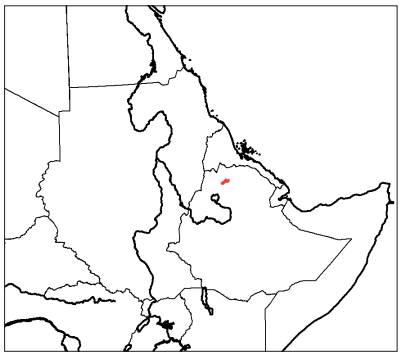
OTHER NAMES Fr. *Bouquetin d'Ethiopie (Le Wali)*; Ger. *Aethiopischer Steinbock* (*Walia-Steinbock).*

MEASUREMENTS HB 150–170cm. T 20–25cm. Sh. ht 90–110cm. W 80-125kg.

RECOGNITION The Walia Ibex has variable tints of russet on the upper limbs and trunk, with dark grey or black on face, neck, dorsal midline, tail and on lower flanks, shoulder and hindquarters. Black and cream patterning of the legs is inconspicuous. Striping on the face is muted by overall darkening. Horns resemble those of the Nubian Ibex but tend to have fewer knobs on their forward surfaces.

GEOGRAPHIC VARIATION None.

DISTRIBUTION The Simien Mts of northern Gondar, NW Ethiopia.



Walia Ibex

HABITAT Mostly above the timberline in the afroalpine and ericaceous zones, between 3000 and 4500m.

FOOD Similar to other goats, feeds on a variety of shrubs and herbs including *Lobelia* and *Erica* species.

BEHAVIOUR Similar to Nubian Ibex, but lived in a richer habitat before being displaced by livestock. Non-territorial. Groups tend to segregate by sex, but sexes mix during pronounced rutting peak between March and May.

ADAPTATIONS Able to traverse and inhabit very steep, arid, rocky terrain. Also withstands extreme cold.

STATUS Total surviving numbers of Walia Ibex have fluctuated between 150 and 750 individuals. Agricultural colonists of Simien National Park, together with their cattle, sheep and goats, have re-invaded the park in recent years, once again threatening the existence of one of Ethiopia's many emblematic endemics. It is urgent that the authorities reverse the irresponsible practices of recent Ethiopian governments and revive good conservation policies in this unique region of Africa.

Respect Africa

Africa is different. We now know, with absolute certainty, that the ecological matrix that is Africa provided that extraordinary cascade of opportunities that culminated in human beings. Africa is our mother-continent.

That makes conservation in Africa fundamentally different from conservation on any other continent. It is to Africa, to its animals, its plants, its landscapes and its succession of existential events, that we must turn to learn about humanity's natural history in all its subtlety, beauty and intelligence.

Respect for subtlety, beauty and intelligence was never a part of Africa's many oppressors and exploiters, past and present. Naked greed for commodities and a total lack of respect for the living fabric of life in Africa, plus deep ignorance, continues to drive events in Africa. Africa has suffered centuries of abuse by pre-colonial, colonial, post-colonial and home-grown despots, bribers, and bribees. The horrors of slavery were linked with plantation agriculture, and the ivory trade has fuelled the slaughter of millions of elephants. It has been said that the darkest thing about the dark continent has always been ignorance of it – ignorance, both cruel and proud, the ignorance of the powerful over the weak, the brutal over the talented, ignorance from within and from without. When it comes to the history and prehistory of humans in Africa the story of continuing ignorance looks more like a perverse conspiracy to silence curiosity itself.

From a conservation perspective, the deepest ignorance concerns the complex ecological interdependencies that have nurtured more than 1,000 mammal species, some 2,500 species of birds, and in South Africa alone, some 45,000 species of plants, around 16,000 of which are endemic to the Cape (for comparison, all of Europe has 12,500 plant species, 28% of which are endemic). Take almost any group of organisms: their diversity in Africa is exceptional. Historically the many natural wonders of the African continent, including its people and all their talents and knowledge, have had scant respect from slavers, colonisers and less obviously culpable powers.

New values emerging

In spite of a tragic history, there are brighter prospects too. To discover a new confidence, pride and respect for Africa and its nature, enter Africa's national parks, its universities and environmental organisations. Here, in the context of new educational institutions, reserves and intensive scientific research, we find the birth of a new and creative culture of environmental involvement. Africa's Naturalists have joined a world-wide web of like-minded people who share an emergent set of values that promise to become truly human, humane and potentially universal. It is also a culture founded upon respect for and action based upon probing analysis of the processes that underlie phenomena. Conservation is not simply about saving mammals or caring for forests. Nor do arguments from science, history, ethics, aesthetics and ecology provide the only rationales in support of it. The tourist industry in Africa is heavily dependent on large mammals as a major educational attraction. Tourism has generated many ancillary industries, including schools, and there is still great scope for investments in conservation and education on both a large and small scale.

Conservation societies and national institutions continue to grow in importance among the more progressive countries of Africa but visionary individuals are still crucial. Those who founded the great national parks and reserves fought real battles with bureaucracies and vested interests. In every case these protagonists were individuals whom we can name. Among Africa's most deserving heroes today are the conservators, wardens, scouts, teachers and researchers who often work under difficult conditions and sometimes live lonely lives. In the parks they care for, the increasing numbers of overseas visitors are actually but a tiny fraction of those who would come if only they had an idea of how much they were missing! Faced with the thrill of seeing Olduvai Gorge or the great fossil sites and living landscapes of South Africa and Ethiopia, scholars, citizens and tourists alike are beginning to travel way beyond glimpses of 'wildlife'. Witnessing such places challenges them to ask why and how our ancestors could have emerged as but one among so many African mammals. Within that quest for self-knowledge a new cultural value is emerging. It is a dawning realisation that the mysteries of human existence are rooted here, in Africa. To know yourself you must get to know Africa.

All modern societies are confronted by questions of values. Personal, communal, national, scientific, religious and material values all jostle for the political stage. Today the most compulsive value is the money you are offered for your work, talents, land, possessions or your captures. This is the value put upon a netted fish or a snared antelope in a market. A zoo-dealer, advertising the same animal in a catalogue, puts a price on every specimen – these are the values of the bazaar – but there are others.

Africa is rich – it is the rest of the World that is poor

The species listed in this guide have no price on them, but continents, countries or parks with the richest variety and greatest numbers are, in a real sense, 'biological millionaires'. On this count, Africa is the richest entity on this globe and North America one of its poorest. A quick flick through the maps in this guide will reveal that some countries are particularly rich while others, such as Algeria, Egypt and Sudan, have already squandered much of their biological inheritance; other countries under irresponsible leadership now look set to follow. Their large mammal populations have gone, are very small or have become totally extinct. Worse still, their people now have so little contact with nature and so little access to scientific education, especially biological knowledge, that the population at large becomes ever more intellectually, scientifically and environmentally impoverished. By contrast, countries like Kenya, Tanzania and Botswana are nurturing an attitude where knowledge and concern for the local environment, local geology, ecology and natural history are coming to be seen as integral to a relevant education and responsible citizenship. Conservation is providing dignified and prestigious livelihoods for sizeable and influential proportions of our citizenry. Income from conservation confers a practical dimension on science and science education in these countries as well as prestige, a situation that is much envied by scientists from less enlightened societies in Africa and elsewhere.

The texts and maps in this guide are a bit like balance sheets, in that we can see *which* species have been lost, stolen or mislaid (sometimes even by *whom*). Maps can show us *where* species have become locally extinct; maps can help alert local people and their governments to just how localised some species are and how uniquely rich some tiny localities are. There are unique centres of endemism, such as around Mongiro springs in Bwamba, Uganda (the only locality in the world to boast 16 species of primates within a 10km radius!), Mounts Oku and Kupe in Cameroon, Udzungwa in Tanzania, Aberdare in Kenya (it is a list that could go on and on).

The worst aspect of Africa's degradation is that it is being promoted by impoverished thinking emanating from continents with impoverished faunas. A typical African landscape easily supports 100 or more mammal species, 400 or 500 bird species and countless other organisms, often adding up to the highest biomasses known on planet Earth. That represents a huge potential for diverse harvests for future human benefit, which seems to have little relevance for the agribusinesses, advisers, 'aid' experts and politicians who are driving the wholesale degradation of Africa. Globally, 75 percent of all agricultural land is used by a handful of domesticated species: cattle, sheep and goats. At the present time that represents 30 percent of Earth's land surface. With ox-eating spreading to ever more ox-eating humans, much of Africa's surface is projected to be converted into giant beef-lots. Yet 'bushmeat' still commands premium prices because indigenous foods are sensed as superior. Of the massive investment that has gone into animal husbandry, effectively none has been spent on the potential for Africa to feed its own on its own resources. This is because the beef is mainly for export, while the 'experts' are mostly non-African imports.

Alerting people to what they are losing is not only a task for this guide, this essay and for the conservation community; there is a real potential for indigenous, rather than foreign, resources being developed within and for Africa. We can reflect on the cultures that have saved or lost their natural resources, especially when savers and losers are immediate neighbours – in general, Kenya has a history of trying to conserve while Somalia destroys. Those who see today's resources as something we borrow from our descendants must condemn the destroyers of once-flourishing mammal populations as thieves or pirates. If we imagine today's disappearing habitats as the subject of future criminal court cases with their destroyers on trial, those in the dock will be out-of-control militias, agribusinesses, the livestock industry, irresponsible or corrupt politicians, logging companies, their accomplices, commercial bushmeat traders and, of course, actual pirates. However, the ultimate blame lies with world appetites for commodities that evade responsibility for environmental costs so long as such goods remain cheap. Curbing the purveyors of such goods

and getting them to support, rather than subvert conservation are among the many dimensions of contemporary conservation in a continent that is unlike any other.

Some of yesterday's 'biological millionaires' are today's destitutes. So, are today's 'biological millionaires' in danger of becoming tomorrow's paupers? Take Tanzania, for example. It has Kilimanjaro, with its unique alpine environments, as well as an extraordinary spectrum of habitats, ranging from forests and swamps to semi-desert. The country's status as one of the most important conservation regions of the world depends upon formal protection for viable and representative samples of every one of these habitats (this a primary target for all national conservation programmes). One of these unique areas is its only 'Somali-arid' sample, a small reserve called Mkomazi. Livestock interests continue trying to wrest this area away from the nation's conservation estate, so far without success. Here a small cabal of cattle-men, with huge herds that they hope to enlarge, threaten a vital asset – the range and depth of Tanzania's biological wealth. They seek to invade a viable ecosystem and impoverish one of the world's most fortunate nations. This is a struggle being played out all over Africa with ever-increasing severity. It is a struggle that began early in the 20th century with formal gazetting of reserves and parks for large mammals. Even then there were people who appreciated the exceptionalism of African fauna and the fact that disappearing mammal populations were clear indicators of wider ecological collapse. Even then conservation had influential opponents.

Learning in the light of nature's own rules

Since then conservation initiatives have greatly diversified and passed through many stages. Today there is more respect for and understanding of the ecological and evolutionary processes that govern all life on earth. Environmental bodies seek to maintain biological diversity, monitor quality and study natural processes. Indeed, comprehending how the planet's ecosystems work is not just a technical challenge; caring for nature in the light of its own rules has become an urgent new moral imperative, imposed on us by our own power over global environments.

In Africa there is the fundamental difference that these were the ecological communities that nurtured the entire course of human evolution. The need to learn, and learn and go on learning about our own history and pre-prehistory, adds practical self-interest and the need for numerous future research projects to the many other justifications for conservation in Africa.

Our self-interest derives from entirely new insights coming from contemporary science. The language of genes, DNA within our eggs and sperm, reveals an unbroken thread of ancestry going back to the beginnings of life on earth. Of that immensely long lineage the mammalian part is relatively small but much of it was spent in Africa. The human part was smaller still but it was shaped in communities of African mammals such as we see today.

Science is not only retrieving our history from fossils and flints, it is re-examining our physiology, our anatomy, our susceptibility to diseases and our behaviour in order to project our past into the future. A picture of the most interesting and complex of all mammals is emerging and there is ever more evidence that the human animal is almost wholly African. Before any of our direct ancestors left Africa we were essentially modern humans. Long before there was agriculture, livestock or industrialisation we possessed qualities we still admire – technical and athletic skills, artistic and musical talents, eloquence, charisma, vivacity and physical beauty.

We became human in a very specific setting – within rich communities of African animals and plants. To destroy those communities is to detach ourselves, irrevocably, from our biological, even our intellectual past. To drift, senseless of our origins, is to impoverish science and medicine, to mythologise and trivialise our culture and to diminish us as descendants of countless generations of intelligent African mammals.

Ecological vandals identified

There is no other continent where the large mammal communities known to our ancestors can still be seen and studied. Eurasia, the Americas and Australia have been emptied of their large mammals and our collective history of vandalising the Earth can only be redeemed by conserving the full spectrum of surviving habitats in our mother continent. Twenty years ago I could still hope that the vision and political will might be found to teach invading cattle-men, loggers and land-grabbers to respect Africa. Instead, the situation has become much worse.

Parts of North Africa that are desert today were once bread-baskets for the Mediterranean. Later, the farming of wheat, corn and cattle spread to the steppes of central Asia, then the prairies of North America, then the pampas of South America: all now support mechanised monocultures on a gigantic scale. The corporate infrastructure behind a now global food (and energy) industry, 'Food Inc.', includes irresponsible banks as well as the manufacturers of machines, chemicals and seeds. Farmers have become its seed-dependent and chemical-dependent serfs. During the last 20 years, in the name of world food-security, agribusinesses have turned to Africa for new land to plough.

It could be argued that the prairies, the pampas and the Asian steppes were already semi-monocultures with impoverished flora and fauna and that ends justified means. That can never be said of Africa. Here, complex, biodiverse ecological communities are deliberately and mindlessly destroyed in their entirety to make way for monoculture crops. But for the technicians and businesspeople that drive 'Food Inc.' one continent is as good as another, given the right breeds, the right seeds, the right chemicals and the right machines. All can be imported if need be – Africa is no different to their own home prairie.

In facing adversaries as insensitive and powerful as 'Food Inc.' and their local political servants, African environmentalists must continue to insist that every major land holder sets aside and maintains between 10 and 20 percent of every holding in reserve for indigenous nature. Furthermore, where such reserves are situated must be determined by informed ecologists, especially wherever springs, headwaters and rivers are involved.

An anticipation of Africa's conversion into farmland has been provided by the logging industry. For centuries Africa's wharves have groaned as cadaverous tree-trunks and the teeth of elephants were levered into the holds of small ships owned by colonial agents. Today the scale of neo-colonial opportunism has vastly enlarged as processions of logging trucks run day and night into the docks of Monrovia, Grand Bassam, Takoradi, Douala, Libreville, Matadi and Luanda, all feeding fleets of giant vessels exporting timber and other raw materials to a greedy world. What does Africa get in return? Cranes, like mechanised Marabou Storks, unload shipment after shipment of bulldozers and trucks, chemicals, chain-saws, automatic assault weapons, short-lived electronic mass-products and luxuries for the elite. Some logging interests pretend that forest communities are renewable after intensive logging. High, climax rainforests are not renewable on any human time-perspective. When the high forests of West Africa are gone, they will, like the elephants of the Ivory Coast, be gone forever.

In general, the scattered and declining status of all natural resources in West, Central, North and north-east Africa reflects official apathy and, sometimes, an incomprehension that sometimes merges into hostility or contempt towards conservation. This attitude has been noted and repeatedly deplored by many concerned and distinguished citizens of those countries, so far with limited effect. Future generations will ask, how could today's governments have permitted extermination of the richest fauna on earth? Dismantling indigenous ecosystems to serve appetites on other continents looks like greedy stupidity today. Tomorrow it may look more like treachery.

The sorcerer's apprentices

A less well-known, but potentially more ominous aspect of the revolution in science and technology has been the application of genetics to the modification of domestic plants and animals. In theory, and increasingly in fact, livestock and crops can be engineered to grow anywhere on earth. For example, buffalo and their immediate ancestors have adapted to the vicissitudes of Africa and its environmental history over several million years. Buffalo genes (or those of any other indigenous organisms that are superior to non-African exotics) can now be patented and inserted into fully controllable and standardised food-producers (like cows or soy beans). Technology-based corporations that seek to standardise and universalise food-production have been quick to initiate, fund, patent and exploit these new applications of genetics.

Conversion of land to agriculture has been greatly speeded up by new chemicals, new techniques, machinery and by the collapse of all sensible restraints on banks and agribusinesses. Thus the most obvious change in Africa over the past 20 years has been hugely accelerated destruction of natural habitats and indigenous biota. In some areas this can be partly explained by great increases in human population but much of the worst destruction is taking place in areas of relatively low population but of great ecological significance. In such cases a lack of any curbs on such destruction has been due to rampant corruption both within and outside Africa. So vast blocks of land have been or are being purchased without any regard for local conservation or the rights of still unpoliticised peoples.

The international press has reported how, in the far north of Mozambique, 2,000 air km from its capital, Maputo, a Japanese/Brazilian conglomerate plans to convert 140,000km^2 into export plantations. This block of land is larger than the whole of England and is home to one of the most independent, original, talented and philosophically minded cultures in all of Africa, that of the Makonde people. The land for this planned plantation also represents one of the largest areas of natural habitats left in all of Africa. Another large-scale and recent land-grab should have taught lessons to its own and to other like-minded perpetrators. In Mali's far north, Libyan agribusiness leased 1,000km^2 of communally owned land from an equally distant government, thereby helping to precipitate a civil war. In Makeni, Sierra Leone, 400km^2 have been leased to a Swiss agribusiness to grow biofuels for export, providing less local earnings and less employment than would a national park (a mere 50 local people employed and profits going to shareholders overseas). These are merely three samples of the 'Second Scramble for Africa'. In spite of coercive tactics exerted by the sponsors and vassals of these vast land-grabs, the associated environmental degradation and loss of control should be a wake-up call to any analytical African thinker or responsible national politician. We *must* put a higher value on our heritage and impose necessary qualifications and restrictions on neocolonial entities bent on creating export-oriented, monoculture plantations. We *must* learn to value the time-tested viability of what is already here and support scientific research into the underlying biological processes that generated the African continent's incomparable biota.

Respect the land and communities that gave us life

Anyone seriously interested in conservation in Africa should become an active member of a conservation society (e.g. the Uganda wildlife clubs, the Ethiopian Natural History Society, or support an international body such as the widely respected WCS and FFI). Ideally every supporter of conservation should become a committed educator combating the deep ignorance of our commercial culture. It is vital that regional pressure groups have support from both within and outside their countries. There are also international conservation societies, each with its own special interests and emphasis. More voices are always required to help put across the case for conserving Africa's animals and their habitats. Above all, new ideas are required on how to achieve conservation aims. Among many encouraging initiatives have been community efforts to save the last natural habitats in the Cape, the creation of island sanctuaries in Lake Victoria (and elsewhere) and reintroductions of 'lost' species to vandalised habitats.

The short history of industrial urbanisation in Africa means that national parks have made a late start on cashing in on the recreational needs of city-dwellers. The world's first national park was described as a 'pleasuring ground' by its founders, who saw it as a sort of zoo-park. For the majority of the citizens of the first industrial societies, city parks, circuses, zoos and playgrounds served as the main places of recreation and escape from the constraints of city life. This is still true but there is more to our environment than a place in which to play.

The users of an early field guide could read without surprise that the mammals of Africa inhabited a 'unique, giant zoo'. When they are not reduced to trophies, meat and leather, African mammals are still often regarded as zoo specimens, now to be gathered up and their genes stored ahead of ecological collapse. Parks are increasingly manipulated by professional managers and there is a risk of mammals and ecological communities becoming domesticated in human minds. That is, perhaps, a greater risk than their actual domestication in man-made enclosures. Given a choice between total extinction and domestication, the latter is surely preferable. In practice, several species of large mammals are candidates for some form of domestication or semi-domesticated ranching: namely Kob and many antelope species, Giant Forest Hogs, rhinoceroses, hippopotamuses, perhaps even elephants.

We do need samples of nature in all its diversity and, yes, we should conserve future gene banks. We can portray mammals as characters on screens or in books, and certainly national parks should be managed for the delight and distraction of the work-weary as well as for research and learning, but there is a still larger issue. If we are not prepared to preserve viable natural habitats for their own sakes, to leave animals and plants spaces of their own, then, in a real sense, we will have lost sight of our place in this world. Parks in Africa will have failed if they do not encourage people to wonder at the natural order of life on Earth and to reflect upon the world beyond civilisation and its physical and mental boundaries, a world beyond grasping human hands where eyes, minds and memories alone can be touched by its eternal mystery and grace.

FURTHER READING

Information on mammals is mostly published in scientific papers. Our sister publication, *Mammals of Africa*, has extensive bibliographies of such papers, as well as comprehensive references for all species.

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There are many important monographs on individual species, families and orders. Books on evolution that are relevant to an understanding of the importance of mammals (especially African mammals) to humanity and the future of humanity include Charles Darwin's *Origin of Species*; Richard Dawkins's *The Ancestors' Tale*, *The Blind Watchmaker* and *The Magic of Reality*; Matt Cartmill & Fred Smith's *The Human Lineage*; Steven Jones's *The Language of the Genes*; Jonathan Kingdon's *Lowly Origin* and *Self-Made Man*; Richard Leakey & Roger Lewin's *Origins Reconsidered*; Christopher Stringer's *African Exodus*; and Edward Wilson's *The Diversity of Life*.

Adult A physically and reproductively mature individual.

Afrotheria A newly recognised taxon (supercohort) of mammals that originated in Africa.

Agouti Grizzled appearance of the coat resulting from alternating light and dark banding of individual hairs.

Allopatry Condition in which populations of different species are geographically separated (reverse of sympatry).

Amphibious Able to live on both land and water.

Anal gland or sac A gland opening either just inside the anus or on either side of it.

Apocrine glands Cutaneous scent glands that produce complex and chemically variable secretions.

Aquatic Applied to animals that live in fresh water. All aquatic mammals move readily on land.

Arboreal Referring to animals that live in trees.

Arthropod The largest phylum in the animal kingdom, including insects, spiders, crabs etc.

Bai Large forest glade, often around a swamp or mere.

Biome A major type of ecological community, such as savanna or desert.

Biotic community A naturally occurring group of plants and animals in the same environment.

Bipedal Two-footed stance or locomotion of four-footed animals.

Bovid A member of the cow-like Bovidae family of the Cetartiodactyla.

Brachydont Low-crowned characteristic of the molars of grazing mammals (opposite of hypsodont).

Brindled Having dark streaks or flecks on a grey or tawny background.

Browser A herbivore that feeds on shoots and leaves of trees, shrubs and forbs.

Bullae (auditory) Globular, bony capsules housing the middle and inner ear structures. Built on to the underside of the skull.

Callosities Patches of thickened skin and tissue (as on the hindquarters of monkeys or knees of some ungulates).

Canine teeth The usually long pointed teeth, one in each quarter of the jaws, that are used by animal-eating mammals for killing their prey.

Catena Series of related events, a biosequence or toposequence.

Carnassial teeth In carnivores, the fourth upper premolar and first lower molar, specialised for shearing meat and sinew.

Carnivore Any meat-eating organism but also a member of the mammal order Carnivora.

Caudal gland An enlarged skin gland associated with the root of the tail. (Subcaudal: below the root; supracaudal: above the root.)

Caecum A blind sac situated at the junction of the small and large intestine, in which digestion of cellulose by bacteria occurs.

Cellulose Main constituent of the cell walls of plants. Very tough and fibrous, and can be digested only by the intestinal flora in mammalian guts.

Cervid A member of the deer family Cervidae, of the Cetartiodactyla.

Cetartiodactyl A member of the order Cetartiodactyla, the even-toed ungulates.

Chablis Tree-fall opening in the forest.

Cheek-pouches A pair of deep pouches extending from the cheeks into the neck skin, present in non-colobine monkeys and some rodents and used for the temporary storage of food.

Cheek-teeth The row of premolars and molars used for chewing food.

Class A taxonomic category. The mammals, Mammalia, are a class.

Colonial Living together in colonies. Notably bats and rodents.

Competitive exclusion Exclusion of one species by another when competing for a common resource.

Concentrate selector A herbivore that feeds on plant parts that are rich in nutrients, such as shoots and fruits.

Conspecific A member of the same species.

Convergence The evolution of similarities between unrelated species occupying similar ecological niches.

Crepuscular Active in twilight.

Crustaceans Members of a class within the phylum Arthropoda, typified by crayfish, crabs and shrimps.

Cryptic Concealing, inconspicuous. Usually referring to coloration and markings.

Cud Partially digested vegetation that a ruminant regurgitates, chews, insalivates and swallows again.

Cursorial Being adapted for running.

Cusp A prominence on a cheek-tooth (premolars or molars).

Dahomey Gap Region or corridor where drier habitats interrupt the forests of West Africa in Togo and Benin.

Dental formula A convention for summarising the dental arrangement whereby the numbers of each type of tooth in each half of the upper and lower jaw are given. The numbers are always presented in the order; incisor (I), canine (C), premolar(P), molar(M). The final figure is the total number of teeth to be found in the skull. A typical example for Carnivora would be 3-1-4-3:3-1-4-3 = 44.

Dentition The arrangement of teeth characteristic of particular species.

Dicot Short for dicotyledon.

Dicotyledon A plant with two seed leaves; the subclass of angiosperms containing most higher plants.

Digit A finger or toe.

Digitigrade Animals that walk on their digits rather than the whole foot.

Dimorphism Two forms, typically the morphological differences between males and females (sexual dimorphism).

Dispersal The movements of animals, often as they reach maturity, away from their previous home-range (equivalent to emigration).

Display Any relatively conspicuous pattern of behaviour that conveys specific information to others, usually to members of the same species: can involve visual and or vocal elements, as in threat, courtship or 'greeting' displays. A behaviour pattern that has been modified (ritualised) by evolution to transmit information by a sender to a receiver.

Diurnal Referring to species that are primarily day-active.

Dorsal The back or upper surface(opposite of ventral).

Dung midden Pile of droppings that accumulate through regular deposits, typically in connection with scent-marking (see also Latrine).

Ecological niche The particular combination of adaptations that fits each species to a place different from that filled by any other species within a community of organisms.

Ecology The scientific study of the interaction of organisms with their environment, including both the physical environment and the other organisms that share it.

Ecosystem A community of organisms together with the physical environment in which they live.

Emigration Departure of animal(s) usually at or about the time of reaching adulthood, from the group or place of birth. Also of biogeographic exchange between continents or regions.

Endemic Native plants and animals.

Eocene Geological epoch 55.8–33.9 mya.

Epidermis The outer layer of the skin or surface tissue of a plant.

Equatorial Geographical region bordering the Equator.

Erg Windswept sandy desert with shifting sand dunes.

False hooves Vestigial nails (digits 2 and 5) that persist in many ruminants as paired hooves or bumps on the fetlock.

Family A taxonomic division subordinate to an order and superior to a genus.

Feral Living in the wild (of domesticated animals, e.g. cat, dog).

Fetlock Joint above the hooves.

Folivore An animal whose diet consists mostly of leaves and other foliage.

Forbs Herbs other than grass that are abundant in grassland, especially during the rains.

Fossorial Adapted for digging.

Frugivore An animal that feeds mainly on fruit.

Fynbo Shrubland of southern Africa with numerous endemic species.

Gallery forest Trees and other vegetation lining watercourses, thereby extending forested habitat into more open zones.

Generalist An animal that is not highly specialised. For example, feeding on a variety of foods that require various foraging techniques.

Genotype The genetic constitution of an organism, determining all aspects of its appearance, structure and function.

Genus (*pl.* **Genera**) A taxonomic division superior to species and subordinate to family.

Gestation The period of development between conception and birth.

Glands Specialised glandular areas of the skin.

Gondwanaland A former land mass that fragmented into Africa and the southern continents in the Mesozoic.

Grazer A herbivore that feeds upon grasses.

Guard hairs The outer coat that overlies the shorter, softer hairs of the underfur (underfur is sparse or absent in many tropical mammals, e.g. most ungulates and primates).

Gumivorous Feeding on gums (plant exudates).

Hammada Stony desert plain.

Hard pan Zone of compacted soil restricting root-growth and drainage.

Harem group A social group consisting of a single adult male, at least two adult females and immature animals.

Herbivore An animal whose diet consists of plant food.

Herd A social group; generally applied to gregarious ungulates.

Hierarchy As applied to social groups, a usually linear rank order in which members dominate all those of lower rank and are dominated by all individuals of higher rank.

Hindgut fermentation Process by which breakdown of cellulose occurs in the caecum and large intestine.

Home-range The area occupied by an individual or group (usually determined by points where the individual(s) is seen over a period of time and plotting the perimeter).

Hypsodont High-crowned characteristic of the molars of grazing mammals (opposite to brachydont).

Hybrid The offspring of parents of different species.

Inguinal Pertaining to the groin.

Insectivore An animal eating mainly arthropods (insects, spiders).

Interdigital Between the digits; e.g. the interdigital (hoof) glands of many antelopes.

Intestinal flora Simple plants(e.g. bacteria) that live in the intestines of mammals. They produce enzymes that break down the cellulose in the leaves and stems of green plants and convert it to digestible sugars.

Invertebrate Animal that lacks a backbone(e.g. insects, spiders, crustaceans).

Juvenile Stage between infant and adult.

Karoo Arid part of the interior plateau in temperate southern Africa. Dominated by dwarf shrubs and adjoined by Highveld grassland.

Keratin Tough fibrous substance of which horns, claws, hooves and nails are composed.

Lactation The secretion of milk from mammary glands.

Larynx Dilated region of upper part of windpipe, containing vocal chords. Vibration of chords produces vocal sounds.

Latrine A place where animals regularly deposit their excrement (see also Midden).
Liana (liane) A vine climbing woody plants; major constituents of rain forest.
Maghreb Loosely defined region of NW Africa.
Mandible The lower jaw.
Maquis Dense secondary scrub dominated by heathers and strawberry trees (Mediterranean).
Masseter A powerful muscle, subdivided into parts, joining the lower and upper jaws, used to bring jaws together when chewing.
Mbuga Valley flat land of clay (black cotton soil), seasonally flooded.
Melanism Darkness of colour due to presence of the black pigment melanin.
Mesozoic Geological era 245–65.5 mya.
Metabolism The chemical processes occurring within an organism, including the production of protein from amino acids, the exchange of gases in respiration and liberation of energy.
Microhabitat The particular parts of the habitat that are encountered by an individual in the course of its activities.
Midden A dung hill or latrine for the regular deposition of faeces by mammals.
Migration Movement, usually seasonal, from one region or climate to another for purposes of feeding or breeding.
Miocene A geographical epoch 23–5.3 mya.
Miombo Woodlands mostly growing on impoverished Precambrian landscapes, with trees dominated by leguminous *Brachystegia* species.
Montane Referring to African mountain habitats, including forest, grassland, bamboo zone, moorland etc.
Morphology Referring to an animal's form and structure.
Mucosa Mucous membrane; a membrane rich in mucous glands such as the lining of the mouth and nasal passage ways.
Mutation A structural change in a gene that can give rise to a new heritable characteristic.
Natural selection Process whereby the fittest genotypes in a population survive to reproduce; a determinant principle in evolution.
mya (*abbrev.*) Million years ago.
Niche The role of a species within the community, defined in terms of all aspects of its life history from food, competitors and predators to all its resource requirements.
Nocturnal Active at night-time.
Nomadic The wandering habit. Among mammals, species that have no clearly defined residence most of the time; distinct from migratory species, which may be resident except when migrating.
Nose-leaf Characteristically shaped flaps of skin surrounding the nasal passages of leaf-nosed bats. Ultrasonic cries are uttered through the nostrils, with the nose-leaves serving to direct the echo-locating pulses forward.
Occipital Pertaining to the occiput at back of head.
Oestrogen Hormone produced by ovaries and responsible for expression of many female characteristics.
Oestrus Behaviour associated with ovulation, being in most mammals the only time when females are sexually receptive ('in heat').
Olfaction, olfactory The olfactory sense is the sense of smell, depending on receptors located in the epithelium, or membrane lining the nasal cavity.
Oligocene A geological epoch 33.9–23 mya.
Omnivorous A mixed diet including both animal and vegetable food.
Opportunistic Referring to animals that capitalise on opportunities to gain food with the least expenditure of energy.
Order A taxonomic division subordinate to class and superior to family.
Ovulation The process of shedding mature ova (eggs) from the ovaries where they are produced.

Paleocene Geological epoch 65.5–55.8 mya.
Parturition The process of giving birth.
Perineal glands Glandular tissue occurring between the anus and genitalia.
Perissodactyl A member of the order Perissodactyla, the odd-toed ungulates.
Pheromone Secretions whose odours act as chemical messengers in animal communication.
Phylogenetic (Of classification or relationship) based on the closeness of evolutionary descent.
Phylogeny A classification or relationship based on the closeness of evolutionary descent. Often portrayed graphically by a branching tree.
Phylum A taxonomic division comprising a number of classes.
Physiology Study of the processes that go on within living organisms.
Pinna The projecting cartilaginous portion of the external ear (especially in bats).
Placenta Structure that connects the foetus and the mother's womb to ensure a supply of nutrients to the foetus and removal of its waste products.
Pleistocene Geological epoch 1.6–0.01 mya.
Pliocene Geological epoch 5.3–1.6 mya.
Polymorphism Occurrence of more than one morphological form of individual in a population.
Population Members of the same species that are within an area at the same time.
Post-partum oestrus Renewed ovulation and mating within days or weeks after giving birth.
Predation The killing and eating of living animal prey.
Predator Any animal that subsists mainly by eating live animals, usually vertebrates.
Preorbital In front of the eye (where a gland occurs in many ungulates).
Presenting The act of directing the hindquarters toward another individual, either in a sexual context or as a gesture of appeasement derived from sexual presenting.
Pronking (also 'stotting') A ritualised bouncy gait in which the animal (usually a bovid) is exceptionally alert.
Protein A complex organic compound made of amino acids. Many different kinds of proteins are present in the muscles and tissues of all mammals.
Proximal Near to the point of attachment or origin.
Quadrupedal Walking on all fours.
Race A subspecies.
Radiation Speciation by a group of related organisms in the process of adapting to different ecological roles.
Rainforest Tropical and subtropical forest with abundant and year-round rainfall. Typically species-rich and diverse.
Range (Geographical)area over which an organism is distributed.
Rank order A hierarchical arrangement of the individuals in a group.
Realm A biogeographic unit encompassing multiple zones and determinant factors.
Relict A persistent remnant population.
Resident Living within a definite, limited home-range, as opposed to being migratory or nomadic.
Reticulum Second chamber of the ruminant cetartiodactyl stomach.
Rinderpest A lethal cetartiodactyl disease.
Ritualisation Evolutionary modification of a behaviour pattern into a display or other signal, through selection for improved communication.
Ritualised Referring to behaviour that has been transformed through the process of ritualisation.
Rodent A member of the order Rodentia, the largest mammalian order, which includes rats and mice, squirrels, anomalures and porcupines.
Rumen First chamber of the ruminant cetartiodactyl stomach. In the rumen the food is liquefied, kneaded by muscular walls and subjected to fermentation by bacteria.

Ruminant A mammal with a specialised digestive system typified by the behaviour of chewing the cud. Its stomach is modified so that vegetation is stored, regurgitated for further maceration, then broken down by symbiotic bacteria. The process of rumination is an adaptation to digesting the cellulose walls of plant cells.

Rut Period of concentrated sexual activity, the mating season.

Sagittal Mid-line over the cranium.

Savanna Vegetation characteristic of tropical regions with extended wet and dry seasons. Dominated by grasses and scattered (predominantly leguminous) trees. The trees vary in type and density from broad-leafed, deciduous woodland in the wetter savanna to grassland with scattered thorn trees and *Acacia* bush grading into subdesert.

Scent gland Area of skin packed with specialised cells that secrete complex chemical compounds that communicate.

Sebaceous glands The commonest type of cutaneous scent glands, consisting of localised concentrations of flask-shaped follicles that produce volatile fatty acids manufactured by symbiotic bacteria.

Sedentary Pertaining to mammals that occupy relatively small home-ranges.

Selection Any feature of the environment that results in natural selection, through differential survival and reproductive success of individuals of differing genetic types.

Sexual dimorphism A condition in which males and females of a species differ consistently in form, size and shape.

Sexual selection Selection of genotypes through competition between members of the same sex (usually males) and mating preferences by members of the opposite sex (usually female).

Sinus A cavity in bone or tissue.

Solitary Unsocial, referring to animals that do not live in social groups.

Speciation The process by which new species arise in evolution. Typically occurs when a single species population is divided by some geographical barrier.

Species Population(s) of closely related and similar organisms that are capable of interbreeding freely with one another, and cannot or normally do not interbreed with members of other species.

Species-specific Characters that serve to distinguish a species, such as its shape, markings or habits.

Spoor Footprints.

Subadult No longer an infant or juvenile but not yet fully adult physically and/or socially.

Subdesert Regions that receive less rainfall than arid zones, but more than true desert.

Subspecies Population(s)that has been isolated from other populations of the same species long enough to develop genetic differences sufficiently distinctive to be considered a separate race.

Superspecies (or species group) A grouping of closely related species.

Swidden Rotational agriculture within rainforest.

Symbiotic A mutually dependent relationship between unrelated organisms that are intimately associated, e.g. the symbiosis between a ruminant and the microorganisms that live in its rumen.

Sympatry Condition of overlapping geographic distribution; applies to related species that coexist without interbreeding (reverse of allopatry).

Systematics The classification of organisms in an ordered system based on their supposed or known natural relationships.

Tarsal Pertaining to the tarsus bones in the ankle, articulating between the tibia and fibia of the leg and the metatarsals of the foot (pes).

Termitary Termite-hill.

Terrestrial Living on land.

Territoriality A system of spacing wherein home-ranges do not overlap randomly – that is, the location of one individual's or group's home-range influences those of others.

Territory An area defended from intruders by an individual or group.

Testosterone A male hormone normally synthesised in the testes and responsible for the expression of many male characteristics.

Thermoregulation The regulation and maintenance of a constant internal body temperature in mammals.

Thoracic Pertaining to the thorax or chest.

Tooth-comb A dental modification in which the incisor teeth form a comb-like structure.

Torpor A dormant state.

Tribe A taxonomic category between family and genus.

Tropical The climate, flora and fauna of the geographic region between 23½° N and S of the Equator. The latitudes reached by the sun at its maximum declination, known respectively as the Tropics of Cancer and Capricorn.

Tsetse fly Two-winged blood-sucking flies, that transmit 'sleeping sickness' (trypanosomiasis) to man and domestic livestock. The flies' presence in the woodlands of Africa south of the Sahara slowed the pace of settlements and thereby preserved habitats for wild animals, which have a natural immunity to tsetse-borne diseases.

Undercoat The soft insulating underfur beneath the longer, coarser guard hairs of the outer coat.

Ungulate A member of one of the orders Cetartiodactyla (even-toed ungulates), Perissodactyla (odd-toed ungulates), Proboscidea (elephants), Hyracoidea (hyraxes) and Tubulidentata (Aardvark), all of which have their feet modified as hooves of various types.

Veld Open uncultivated grassland in southern Africa.

Ventral The underside, lower surface of an animal, opposite to dorsal.

Vertebrate An animal with a spinal column and skeleton of bone, including amphibians, reptiles, birds and mammals.

Vestigial A characteristic with little or no contemporary use, but derived from one that was useful and well developed in an ancestral form or period.

Vibrissae Stiff, coarse hairs richly supplied with nerves, found especially around the snout and with a sensory (tactile) function.

Vocalisation Calls or sounds produced by the vocal chords of a mammal, and uttered through the mouth. Vocalisations differ with the age and sex of mammals but are usually similar within a species.

Watershed Elevated land between drainage basins.

Yearling A young animal between one and two years of age (referring to species that take at least two years to mature).

INDEX

Aardvark 86
Aardwolf 428
Acinonyx jubatus 403
Acomys 272
Addax 614
Addax nasomaculatus 614
Aepyceros melampus 590
Aepycerotini 590
Aethomys 295
Afroinsectiphillia 68–88
Afrosoricida 68–75
Afrotheres 48–88
Afrotheria 48–88
alcelaphines 592
Alcelaphini 592
Alcelaphus buselaphus (incl. *lichtensteinii*) 598
Allactaga tetradactyla 257
Allenopithecus 143
Allenopithecus nigroviridis 143
Allochrocebus group 154–155
Allochrocebus lhoesti 155
Allochrocebus preussi 156
Allochrocebus solatus 157
Allosciurus aubinnii 229
Amblysomus 75
Ammodile 279
Ammodillus imbellis 279
Ammodorcas clarkei 568
Ammotragus lervia 615
Angwantibo, Calabar 188
  Golden 189
Anomalure, Beecroft's 253
  Lesser 252
  Lord Derby's 251
  Pel's 252
anomalures 249–251
Anomaluridae 249–255
Anomalurus beecrofti 253
Anomalurus derbianus 251
Anomalurus peli 252
Anomalurus pusillus 252
Antelope, Dwarf 525
  Roan 605
  Royal 524
  Sable 607
antelopes 522–524
  dwarf 524
  gazelline 557–558
  horse-like 605
Antidorcas marsupialis 571
Antilopinae 522–618
Antilopini 557–558
Aonyx capensis 387
Aonyx congicus 386
Apodemus sylvaticus 282
Arctocebus aureus 189
Arctocebus calabarensis 188
Arctocephalus 388
Arctocephalus pusillus 388
Arvicanthis 302
Asellia 341
Ass, African Wild 469
Atelerix 311
Atherurus africanus 217
Atilax paludinosus 433
Atlantoxerus getulus 245

baboon-mangabeys 124–125
Baboon, Chacma 121
  Guinea 119
  Olive 120
  Sacred 118
  Yellow 121
baboons 117–118
Barbastella 356
Bat, African Leaf-nosed 342
  African Sheath-tailed 344
  Badger 357
  Barbastelle 356
  Black-hawk 345
  Butterfly 356
  East African Flat-headed 348
  Evening 354
  Flat-headed 348
  Giant Mastiff 349
  Guano 346
  Hairy 353
  Heart-nosed 338
  Hemprich's Long-eared 355
  Horseshoe 339
  House 354
  Leaf-nosed 340
  Long-eared 355
  Long-fingered 350
  Moloney's Flat-headed 358
  Mops Free-tailed 347
  Mouse-tailed 337
  Nectar 331
  Noctule 359
  Percival's Trident 341
  Pimple-winged 351
  Pipistrelle 359
  Roberts's Flat-headed 349
  Schlieffen's Twilight 355
  Serotine 358
  Slit-faced 343
  Tomb 344
  Trident leaf-nosed 341
  Tropical Long-eared 357
  Winged-mouse 348
  Woolly 353
  Wrinkle-lipped 347
  Yellow-winged 338
Bathyergidae 221–223
Bathyergus 222
bats 322–324
  free-tailed 346
  fruit 325–327
  horseshoe 339
  large-winged 337
  leaf-nosed 340
  long-fingered 350
  mouse-tailed 337
  pimple-winged 351
  sheath-tailed 344
  slit-faced 342–343
  vesper 351–353
Bdeogale 441–442
Bdeogale crassicauda 442
Bdeogale jacksoni 444
Bdeogale nigripes 443
Bdeogale omnivora 442
Beamys hindei 262
Beatragus hunteri 593
Beira 551
Blesbok 594
Blesmol, Cape 222
  Common 223
  Dune 222
  Silky 221
blesmols 221
Boar, Wild 477
Bongo 517
Bonobo 97
Bontebok 594
Bovidae 500–618
bovids 500–502
Bovinae 502–521
bovines 502
  spiral-horned 505–506
Bovini 502
Buffalo, African 503
Bunolagus monticularis 307
bushbabies *see* galagos
Bushbuck 513
Bushpig 478

Calcochloris 71

Cane Rat, Marsh 220
  Savanna 219
Canidae 363–377
Caniformia 363–390
Canis adustus 367
Canis aureus 370
Canis lupus 371
Canis mesomelas 368
Canis pictus 365
Canis simensis 369
Capra nubiana 617
Capra walie 618
Caprini 615
Caracal 401
Caracal caracal 401
Cardioderma cor 338
Carnivora 360–454
carnivores 360–363
Carpitalpa arendsi 75
Casinycteris 329
Cat, African Golden 400
  Black-footed 406
  Sand 407
  Swamp 405
Catarrhini 90–184
cats 391, 393–394
Cephalophini 527–529
Cephalophus 533–534
Cephalophus adersi 536
Cephalophus callipygus 542
Cephalophus dorsalis 545
Cephalophus harveyi 538
Cephalophus jentinki 546
Cephalophus leucogaster 537
Cephalophus natalensis 538
Cephalophus niger 543
Cephalophus nigrifrons 540
Cephalophus ogilbyi 540
Cephalophus rubidus 537
Cephalophus rufilatus 539
Cephalophus silvicultor 544
Cephalophus spadix 543
Cephalophus weynsi 541
Cephalophus zebra 535
Ceratotherium simum 473
Cercocebus 132–133
Cercocebus agilis 136
Cercocebus atys 135
Cercocebus chrysogaster 133
Cercocebus galeritus 136
Cercocebus lunulatus 134
Cercocebus sanjei 137
Cercocebus torquatus 134
Cercopithecidae 100–184
Cercopithecinae 116–184
Cercopithecini 139–184
Cercopithecoidea 100–184
Cercopithecus 158
Cercopithecus (cephus) ascanius 183
Cercopithecus (cephus) cephus 181
Cercopithecus (cephus) erythrogaster 179
Cercopithecus (cephus) erythrotis 182
Cercopithecus (cephus) group 177–178
Cercopithecus (cephus) petaurista 179
Cercopithecus (cephus) sclateri 180
Cercopithecus (diana) diana 159
Cercopithecus (diana) group 159
Cercopithecus (diana) roloway 160
Cercopithecus (dryas) dryas 158
Cercopithecus (dryas) group 158
Cercopithecus (dryas) salongo 159
Cercopithecus (hamlyni) group 169–170
Cercopithecus (hamlyni) hamlyni 170
Cercopithecus (hamlyni) lomamiensis 171
Cercopithecus (mona) campbelli 165
Cercopithecus (mona) denti 166
Cercopithecus (mona) group 163–164
Cercopithecus (mona) lowei 165
Cercopithecus (mona) mona 164
Cercopithecus (mona) pogonias 168
Cercopithecus (mona) wolfi 167
Cercopithecus neglectus 161
Cercopithecus (nictitans) group 172–173
Cercopithecus (nictitans) mitis 175
Cercopithecus (nictitans) nictitans 174
Cervidae 499–500
Cervus elaphus 499
Cetartiodactyla 475–618
Chaerophon 347
Cheetah 403
Chevrotain, Water 490
chevrotains 490
Chimpanzee, Common 95
  Gracile 97
Chiroptera 322–359
Chlorocebus aethiops 150
Chlorocebus djamdjamensis 152
Chlorocebus group 148–150
Chlorocebus pygerythrus 151
Chlorocebus sabaeus 152
Chlorocebus tantalus 151
Chlorotalpa 75
Choeropsis liberiensis 489
Chrysochloridae 70–75
Chrysochloris 74
Chrysospalax 71
Cistugidae 351
Cistugo 351
Civet, African 409
  Tree 391
civets 408–409
Civettictis civetta 409
Cloeotis percivali 341
Coleura afra 344
Colobinae 101–115
Colobus, Angola 112
  Black 111
  Central African Red 107
  Eastern Red 107
  Geoffroy's 114
  Guereza 114
  King 112
  Niger Delta Red 109
  Olive 102
  Pennant's Red 108
  Preuss's Red 109
  Tana River Red 106
  Tshuapa Red 107
  Udzungwa Red 105
  Waldron's Red 110
  Western Red 110
  Zanzibar Red 105
Colobus 111
Colobus abyssinicus 114
Colobus angolensis 112
Colobus guereza 114
Colobus polykomos 112
Colobus satanus 111
Colobus vellerosus 114
Colomys 286
Congosorex 316
Connochaetes gnou 603
Connochaetes taurinus 601
Cricetidae 267

Cricetomys 263
Crocidura 319
Crocuta crocuta 426
Crossarchus 449
Crossarchus alexandri 451
Crossarchus ansorgei 450
Crossarchus obscurus 450
Crossarchus platycephalus 451
Cryptochloris 74
Cryptomys 223
Ctenodactylidae 214–216
Ctenodactylus 214
Cusimanse, Alexander's 451
  Ansorge's 450
  Cameroon 451
  Common 450
Cusimanses 449
Cynictis penicillata 437
Cynictis selousi see *Paracynictis selousi*

Damaliscus pygargus 594
Damaliscus lunatus 596
Dasymys 298
Deer 499
  Red 499
Delanymys brooksi 261
Dendrohyrax arboreus 54
Dendrohyrax dorsalis 55
Dendrohyrax validus 53
Dendromus 265
Dendroprionomys rousseloti 265
Deomyinae 271–273
Deomys ferugineus 271
Dephomys defua 295
Desmodilliscus braueri 275
Desmodillus auricularis 275
Desmomys 299
Dibatag 568
Diceros bicornis 471
Dikdik, Damara 555
  Günther's 556
  Kirk's 555
  Naivasha 555
  Salt's 554
  Silver 554
  Ugogo 555
dikdiks 552–553
Dipodidae 257–258
Dog, African Wild 365
  Hunting 365
dogs and allies 363–365
Dologale dybowski 452
Dorcatragus megalotis 551
Dormice 246
Dormouse, African 248
  African Rock 247
  Orchard 249
  Small-eared 247
  West African Smoky 246
Drill 130
drill-mangabeys 132–133
Dugong 64
Dugong dugon 64
Dugongidae 64–66
Duiker, Abbott's 543
  Aders's 536
  Bay 545
  Black 543
  Black-fronted 540
  Blue 530
  Bush 532
  Harvey's 538
  Jentink's 546
  Maxwell's 531
  Natal Red 538
  Ogilby's 540
  Peters's 542
  Red-flanked 539
  Rwenzori Red 537
  Walter's 531
  Weyns's 541
  White-bellied 537
  Yellow-backed 544
  Zebra 535
duikers 527–529
  blue 529
  forest 533–534

Eidolon helvum 328
Eland, Common 519
  Giant 518
elephant-shrews *see* sengis
Elephant, Bush 59
  Forest 58
Elephantidae 57–63
Elephantulus 78
Eliomys 249
Emballonuridae 344–345
Epixerus ebii 230
Epixerus wilsoni 230
Epomophorus 335
Epomops 333
Eptesicus 358
Equidae 461–470
Equus 462–463
Equus africanus 469
Equus grevyi 463
Equus quagga 465
Equus zebra 467
Eremitalpa granti 73
Erinaceidae 311–313
Erinaceomorpha 311–313
Erythrocebus 147
Erythrocebus patas 147
Eudorcas albonotata 563
Eudorcas rufifrons 562
Eudorcas thomsoni 563
Eudorcas tilonura 563
Euoticus 206–207
Euoticus elegantulus 207
Euoticus pallidus 207

Felidae 393–408
Feliformia 391–454
Felis chaus 405
Felis margarita 407
Felis nigripes 406
Felis sylvestris 405
Felovia vae 215
Flying Calf 334
flying-foxes 327
Fox, Bat-eared 372
  Cape 374
  Fennec 373
  Pale 375
  Red 376
  Royal 373
  Rüppell's 375
Fruit Bat, Angola 330
  Benguela 334
  Collared 331
  Dwarf Epauletted 335
  Epauletted 335
  Golden 329
  Hammer-headed 332
  Mountain 330
  Singing 333
  Straw-coloured 328
  Tear-drop 328
fruit bats 325–327
Funisciurus 231
Funisciurus anerythrus 233
Funisciurus bayonii 232
Funisciurus carruthersi 231
Funisciurus congicus 236
Funisciurus duchaillui 235
Funisciurus isabella 235
Funisciurus lemniscatus 232

Funisciurus leucogenys 233
Funisciurus pyrropus 234
Funisciurus substriatus 234

Galagidae 190–211
Galago, Allen's Squirrel 201
  Demidoff's 195
  Diani 198
  Elegant 207
  Gabon Squirrel 202
  Greater 204
  Makandé Squirrel 202
  Mozambique 198
  Pallid 207
  Rondo 199
  Senegal 210
  Small-eared 205
  Somali 211
  Southern 210
  Spectacled 209
  Thomas's 195
  Usambara 197
  Zanzibar 200
Galago 208–209
Galago gallarum 211
Galago inustus 209
Galago matschiei 209
Galago moholi 210
Galago senegalensis 210
Galagoides 194
Galagoides cocos 198
Galagoides demidoff 195
Galagoides granti 198
Galagoides orinus 197
Galagoides rondoensis 199
Galagoides thomasi 195
Galagoides zanzibaricus 200
galagos 190–193
  dwarf 194
  east coast dwarf 197, 199
  equatorial dwarf 194
  greater 203–204
  lesser 208–209
  montane dwarf 197
  needle-clawed 206–207
  squirrel 201
Gazella cuvieri 561
Gazella dorcas 559
Gazella leptoceros 561
Gazella spekei 560
Gazelle, Bright's 564
  Cuvier's 561
  Dama 566
  Dorcas 559
  Eritrean 563
  Grant's 564
  Mongalla 563
  Red-fronted 562
  Rhim 561
  Soemmerring's 565
  Speke's 560
  Tana 564
  Thomson's 563
gazelles 558–559
Gelada 127
Genet, Aquatic 415
  Blotched 419
  Bourlon's 421
  Cape 418
  Common 416
  Crested 414
  Ethiopian 412
  Feline 417
  Giant 413
  Hausa 413
  Johnston's 415
  King 420
  Miombo 418
  Pardine 419
  Servaline 414
genets 408–409, 412
Genetta 412
Genetta abyssinica 412
Genetta angolensis 418
Genetta bourloni 421
Genetta cristata 414
Genetta felina 417
Genetta genetta 416
Genetta johnstoni 415
Genetta maculata 419
Genetta pardina 419
Genetta piscivora 415
Genetta poensis 420
Genetta servalina 414
Genetta thierryi 413
Genetta tigrina 418
Genetta victoriae 413
Georychus capensis 222
Gerbil 278
  Brauer's Dwarf 275
  Fat-tailed 274
  Hairy-footed 280
  Namaqua 275
  Peel's Pygmy 278
  Robust 279
  Slender 275
Gerbillinae 274–280
Gerbilliscus 279
Gerbillurus 280
Gerbillus 278
gerbils 274
Gerenuk 569
Giraffa (camelopardalis) 492
Giraffe 492
giraffes 492
Giraffidae 492–498
Glauconycteris 356
Gliridae 246–249
Gnu, Brindled 601
  White-tailed 603
goats 615
Golden-mole, Arends's 75
  Cape 74
  Congo 74
  Cryptic 74
  Desert 73
  Forty-toothed 75
  Giant 71
  Lesser Narrow-headed 75
  Narrow-headed 75
  Stuhlmann's 74
  Yellow 71
golden-moles 70–71
  key to 72–73
Gorilla, Eastern 93
  Western 91
Gorilla beringei 93
Gorilla gorilla 91
Grammomys 297
Graphiurus (Aethoglis) nagtaglasi 246
Graphiurus (Claviglis) 247
Graphiurus (Gliriscus) 247
Graphiurus (Graphiurus) 248
Grysbok, Cape 548
  Sharpe's 548
grysboks 548
guenons 139–142
  arboreal 158
Gundi, Fringe-eared 216
  Senegal 215
gundis 214

Hare, Abyssinian 309
  Cape 309
  Ethiopian 309
  Savanna 310
  Scrub 309
  Starck's 310

hares, true 308
Hartebeest 598
Hedgehog, African 311
  Desert 313
  Long-eared 312
hedgehogs 311
Heimyscus fumosus 288
Heliophobius argenteocinereus 221
Heliosciurus 225
Heliosciurus gambianus 227
Heliosciurus mutabilis 226
Heliosciurus punctatus 228
Heliosciurus rufobrachium 227
Heliosciurus ruwenzori 225
Heliosciurus undulatus 226
Helogale hirtula 453
Helogale parvula 453
Hemiechinus auritus 312
Herpestes flavescens 436
Herpestes ichneumon 434
Herpestes ochraceus 437
Herpestes pulverulenta 436
Herpestes sanguineus 435
Herpestidae 430–454
Herpestinae 432–444
Heterocephalidae 224
Heterocephalus glaber 224
Heterohyrax brucei 52
Hippopotamidae 486–490
Hippopotamus, Common 487
  Pygmy 489
Hippopotamus amphibius 487
hippopotamuses 486–487
Hipposideridae 340–342
Hipposideros 340
Hippotragini 605
Hippotragus equinus 605
Hippotragus niger 607
Hirola 593
Hog, Giant Forest 480
  Red River 479
Hominidae 90–100
Hominini 99–100
horses 461–462
  African 462–463
Huetia leucorhinus 74
Hyaena brunnea 424
Hyaena hyaena 423
Hyaena, Brown 424
  Spotted 426
  Striped 423
Hyaenidae 421–429
hyaenids 421–422
Hybomys group 294
Hydrictis maculicollis 384
Hyemoschus aquaticus 490
Hylochoerus meinertzhageni 480
Hylomyscus 289
Hypsignathus monstrosus 332
Hyracoidea 49–55
Hyrax, Bush 52
  Eastern Tree 53
  Rock 51
  Southern Tree 54
  Western Tree 55
hyraxes 50
Hystricidae 216–218
Hystrix africaeaustralis 218
Hystrix cristata 217

Ibex, Nubian 617
  Walia 618
Ichneumia albicauda 439
Ictonyx striatus 381
Idiurus macrotis 254
Idiurus zenkeri 254
Impala 590

Jackal, Black-backed 368
  Common 370
  Side-striped 367
Jaculus 258
Jerboa, Desert 258
  Four-toed 257
Jird 277
  Bushy-tailed 277

Kerivoula 353
Kilimatalpa stuhlmanni 74
Kipunji 122, 123
Klipspringer 588
Kob 581
kobs 574–576, 581
Kobus ellipsiprymnus 586
Kobus kob 581
Kobus leche 583
Kobus megaceros 585
Kobus vardoni 583
Kudu, Greater 511
  Lesser 507

Laephotis 357
Lagomorpha 303–310
Lamottemys okuensis 293
Lavia frons 338
Lechwe, Nile 585
  Southern 583
Leimacomyinae 273
Leimacomys buettneri 273
Lemniscomys 301
Leopard 397
Leporidae 304–310
Leptailurus serval 398
Lepus 308
Lepus capensis 309
Lepus crawshayi 309
Lepus fagani 309
Lepus habessinicus 309
Lepus saxatilis 309
Lepus starcki 310
Lepus victoriae 309
Liberiictis kuhni 448
Linsang, Central African 410
  West African 411
Lion 394
Liotomys see *Myotomys*
Lissonycteris angolensis 330
Litocranius walleri 569
Lophiomyinae 268–270
Lophiomys imhausi 270
Lophocebus 124–125
Lophocebus albigena 125
Lophocebus aterrimus 126
Lophuromys 272
Lorisidae 186–190
Loxodonta africana 59
Loxodonta cyclotis 58
Lutra lutra 385
Lutrinae 383–388

Macaca 138
Macaca sylvanus 138
Macaque, Barbary 138
macaques 138
Macroscelidea 76–85
Macroscelides proboscideus 78
Macroscelidinae 76–79
Madoqua 552–553
Madoqua guentheri 556
Madoqua (kirkii) cavendishi 555
Madoqua (kirkii) damarensis 555
Madoqua (kirkii) kirkii 555
Madoqua (kirkii) thomasi 555
Madoqua piacentinii 554
Madoqua saltiana 554
Madoquini 552
Malacomys 286
Malacothrix typica 264
Manatee, West African 67
manatees 66
Mandrill 129

Mandrillus leucophaeus 130
Mandrillus sphinx 129
Mangabey, Agile 136
Black 126
Golden-bellied 133
Grey-cheeked 125
Red-capped 134
Sanje 137
Sooty 135
Tana River 136
White-naped 134
Manidae 455–460
Massouteria mzabi 216
Mastomys 287
Meerkat 445
Megadendromus nicolausi 266
Megadermatidae 337–339
Megaloglossus woermanni 331
Mellivora capensis 378
Meriones 277
Mesopotamogale ruwenzorii 70
Micaelamys 296
Microdillus peeli 278
Micropotamogale lamottei 69
Micropteropus 335
Microtus guentheri 267
Mimetillus moloneyi 358
Miniopteridae 350
Miniopterus 350
Miopithecus ogouensis 145
Miopithecus talapoin 146
Mole-rat, Dune 222
Naked 224
Palestine 259
Silvery 221
Molossidae 346–350
Monachus 390
Monachus monachus 390
Mongoose, Angola Slender 436
Banded 446
Black-legged 443
Bushy-tailed 442
Dwarf 453
Gambian 448
Ichneumon 434
Jackson's 444
Liberian 448
Long-snouted 432
Marsh 433
Meller's 440
Savanna 452
Selous's 438
Slender 435
Small Grey 436
Sokoke Dog 442
Somali Dwarf 453
Somali Slender 437
White-tailed 439
Yellow 437
mongooses 430–432
common 434
dog 441–442
four-toed 441–442
social 444–445
solitary 432
Monkey, Allen's Swamp 143
Bale 152
Campbell's 165
Crowned 168
De Brazza's 161
Dent's 166
Diana 159
Dryad 158
Gentle 175
Green 152
Grivet 150
L'Hoest's 155
Lesser Spot-nosed 179
Lesula 171
Lowe's 165
Mona 164
Moustached 181
Owl-faced 170
Patas 147
Preuss's 156
Putty-nosed 174
Red-eared 182
Red-tailed 183
Roloway 160
Salongo 159
Sclater's 180
Sun-tailed 157
Tantalus 151
Vervet 151
White-throated 179
Wolf's 167
monkeys, cephus 177–178
cheek-pouched 116–117
colobus 101–102
diana 159
dryad 158
gentle 172–173
long-faced 169–170
mona 163–164
mountain 154–155
Old World 100–101
pied colobus 111
red colobus 103–105
savanna 148–150
Mops 347
Mormopterus 348
Mouse, African Climbing 265
African Wood 289
Bates's Climbing 265
Brush-furred 272
Climbing 264
Common 282
De Balsac's 288
Delaney's 261
Fat 264
Four-striped Grass 299
Giant Climbing 266
Hump-nosed 294
Large-eared 264
Long-eared Flying 254
Long-tailed Field 282
Meadow 285
Namaqua Rock 296
Pouched 263
Pygmy Rock 261
Spiny 272
Togo 273
Uranomys 271
Velvet Climbing 265
White-tailed 262
Wurch 283
Zebra 301
Zenker's Flying 254
Mungos gambianus 448
Mungos mungo 446
Mungotinae 444–449
Muriculus imberbis 283
Muridae 268–302
murids 268
Murinae 280–302
murines, African herbivorous 289–302
African omnivorous 284–289
recent immigrant 281–283
Muroidea 257
muroids, archaic 260–266
cricetid 267
Mus 282
Mustela nivalis 380
Mustela putorius 380
Mustelidae 377–388
mustelids 377–378
Mylomys 300
Myomorpha 257–302
Myomyscus ('*Myomys*') 285
Myonycteris 331

Myopterus 348
Myosciurus pumilio 228
Myosorex 315
Myotis 353
Myotomys 291
Myoxidae *see* Gliridae
Mystromys albicaudatus 262

Nandinia binotata 391
Nandiniidae 391–392
Nanger dama 566
Nanger (granti) granti 564
Nanger (granti) notata 564
Nanger (granti) petersi 564
Nanger soemmerringi 565
Nanonycteris veldkampi 334
Neamblysomus 75
Neotragini 524
Neotragus batesi 525
Neotragus pygmaeus 524
Nesokia indica 281
Nesomyidae 260–266
nesomyids, 'dendromurine' 264–266
  cricetomyine 262–264
Nesotragus moschatus 526
Niumbaha superba 357
Noctule 359
Noki 220
Nyala 508
  Mountain 510
Nyctalus 359
Nycteridae 342–343
Nycteris 343
Nycticeinops schlieffeni 355

Oenomys 293
Okapi 497
Okapia johnstoni 497
Oreotragini 588
Oreotragus oreotragus 588
Oribi 573
Orycteropodidae 86–88
Orycteropus afer 86
Oryctolagus cuniculus 307
Oryx, Beisa 610
  Scimitar-horned 609
  Southern 612
Oryx beisa 610
Oryx dammah 609
Oryx gazella 612
Osbornictis piscivora see *Genetta piscivora*
Otariidae 388–389
Otocyon megalotis 372
Otolemur 203–204
Otolemur crassicaudatus 204
Otolemur garnettii 205
Otomops martiensseni 349
Otomyini 290–292
Otomys 291
Otonycteris hemprichii 355
Otter-shrew, Giant 69
  Mount Nimba 69
  Rwenzori 69
otter-shrews 69
Otter, African Clawless 387
  Common 385
  Congo Clawless 386
  Spotted-necked 384
otters 383–384
Ourebia ourebi 573
Ourebini 573
Oxen 502
Oyan, Central African 410
  West African 411
oyans 410

Pachyuromys duprasi 274
Paenungulata 48–68
Pan paniscus 97
Pan troglodytes 95
Pangolin, Giant 458
  Ground 459
  Long-tailed 456
  Tree 457
pangolins 455–456
Panthera leo 394
Panthera pardus 397
Papio 117–118
Papio anubis 120
Papio cynocephalus 121
Papio hamadryas 118
Papio papio 119
Papio ursinus 121
Paracrocidura 319
Paracynictis selousi 438
Paraechinus aethiopicus 313
Paraxerus 236–237
Paraxerus alexandri 237
Paraxerus boehmi 238
Paraxerus cepapi 240
Paraxerus cooperi 237
Paraxerus flavovittis 239
Paraxerus (lucifer) byatti 241
Paraxerus (lucifer) group 240
Paraxerus (lucifer) laetus 241
Paraxerus (lucifer) lucifer 240
Paraxerus (lucifer) vexillarius 241
Paraxerus ochraceus 239
Paraxerus palliatus 242
Paraxerus poensis 238
Paraxerus vincenti 242
Parotomys 290
Pectinator 215
Pectinator spekei 215
Pedetes 256
Pedetidae 255–256
Pelea capreolus 576
Pelomys 300
Perissodactyla 461–474
Perodicticus potto 186
Petrodromus tetradactylus 77
Petromuridae 220–221
Petromus typicus 220
Petromyscus 261
Phacochoerus 482
Phacochoerus aethiopicus 483
Phacochoerus africanus 484
Phataginus tricuspis 457
Philantomba 529
Philantomba maxwelli 531
Philantomba monticola 530
Philantomba walteri 531
Phocidae 389–390
Pholidota 455–460
pigs 476
Piliocolobus 103–105
Piliocolobus badius 110
Piliocolobus epieni 109
Piliocolobus gordonorum 105
Piliocolobus kirkii 105
Piliocolobus oustaleti 107
Piliocolobus pennantii 108
Piliocolobus preussi 109
Piliocolobus rufomitratus 106
Piliocolobus tholloni 107
Piliocolobus waldronae 110
Pinnipedia 388–390
Pipistrelle 359
Pipistrellus 359
Platymops setiger 348
Plecotus 355
Plerotes anchietae 334
Poecilictis libyca 381
Poecilogale albinucha 382
Poelagus marjorita 304
Poiana 410
Poiana leightoni 411
Poiana richardsoni 410
Polecat 380

Porcupine, Brush-tailed 217
Crested 217
South African 218
porcupines 216
Potamochoerus larvatus 478
Potamochoerus porcus 479
Potamogale velox 69
Potamogalinae 69–70
Potto, Common 186
Martin's 188
Praomys 285
Primates 89–211
Prionomys batesi 265
Proboscidea 56–63
proboscids 56
Procavia 51
Procaviidae 50–55
Procolobus verus 102
Profelis aurata 400
Pronolagus 304
Pronolagus crassicaudatus 306
Pronolagus randensis 306
Pronolagus rupestris 305
Pronolagus saundersiae 305
Prosimians 185–211
Proteles cristata 428
Protelinae 428–429
Protoxerus stangeri 229
Psammomys 276
Pseudopotto martini 188
Pteropodidae 325–327
Pteropus 327
Puku 583

Rabbit, Bunyoro 304
Common 307
Riverine 307
Raphicerini 548
Raphicerus campestris 549
Raphicerus melanotis 548
Raphicerus sharpei 548
Rat, Acacia 297
Black 281
Broad-footed Thicket 294
Broad-headed Stink 287
Bush 295
Cape Ice 291
Creek 300
Crested 270
Dassie 220
Defua 295
Dega 299
Ethiopian Meadow 288
Giant Pouched 263
Grass 302
Groove-toothed 291
Lesser Pouched 262
Link 271
Long-footed 286
Maned 270
Mill 300
Mount Oku 293
Multimammate 287
Narrow-footed Thicket 297
Rusty-nosed 293
Sand 276
Shaggy Swamp 298
Short-tailed Bandicoot 281
Soft-furred 285
Swamp 286
Target 295
Velvet 286
Whistling 290
Ratel 378
rats, cane 219
hair-modified 271
pouched 262
Rattus rattus 281
Redunca arundinum 580
Redunca fulvorufula 578
Redunca redunca 579
reduncines 574–576
Reduncini 574–576
Reedbuck, Bohor 579
Mountain 578
Southern 580
reedbucks 578
Rhabdomys pumilio 299
Rhebok 576
Rhinoceros, Black 471
White 473
rhinoceroses 470–471
Rhinocerotidae 470–474
Rhinolophidae 339–340
Rhinolophus 339
Rhinopoma 337
Rhinopomatidae 337
Rhynchocyon chrysopygus 84
Rhynchocyon cirnei 85
Rhynchocyon petersi 84
Rhynchocyon sp. nov. 81
Rhynchocyon udzungwensis 81
Rhynchocyoninae 80–85
Rhynchogale melleri 440
Rock-hare, Hewitt's Red 305
Jameson's Red 306
Natal Red 306
Smith's Red 305
rock-hares 304
Rodentia 212–302
rodents 212–213
Root-rat 259
Rousette, Egyptian 329
Rousettus aegyptiacus 329
Ruminantia 490–618
ruminants 490
Rungwecebus 122–123
Rungwecebus kipunji 123
Ruwenzorisorex suncoides 318

Saccolaimus peli 345
Saccostomus 263
Sand-puppy 224
Sauromys petrophilus 349
Scaly-tail, Cameroon 255
Sciuridae 225–245
Sciurocheirus 201
Sciurocheirus alleni 201
Sciurocheirus gabonensis 202
Sciurocheirus makandensis 202
Scotoecus 354
Scotonycteris zenkeri 328
Scotophilus 354
Scutisorex 317
sea-cows 64
Seal, Cape Fur 388
Mediterranean Monk 390
seals 388
fur 388
monk 390
true 389
Sekeetamys calurus 277
Sengi, Black-and-rufous Giant 84
Chequered Giant 85
Four-toed 77
Golden-rumped Giant 84
Lesser 78
Mandela's Giant 81
Round-eared 78
Udzungwa Giant 81
sengis 76
giant 80
soft-furred 76–77
Serval 398
sheep 615
Sheep, Barbary 615
Shrew, Congo 316
Forest 317
Hero 317
Mole 315
Mouse 315
Musk 316

Shrew *continued*
Rodent 319
Rwenzori Water 318
White-toothed 319
shrews 314–315
Sirenia 64–68
Sitatunga 515
Smutsia gigantea 458
Smutsia temminckii 459
Soricidae 314–321
Soricomorpha 314–321
Spalacidae 259–260
Spalax ehrenbergi 259
Springbok 571
Springbuck 571
springhares 255–256
Squirrel, African Giant 229
African Pygmy 228
Alexander's Bush 237
Barbary Ground 245
Biafran Bight Palm 230
Böhm's Bush 238
Carruthers's Mountain 231
Congo Rope 236
Cooper's Mountain 237
Damara Ground 243
Du Chaillu's Rope 235
Fire-footed Rope 234
Gambian Sun 227
Green Bush 238
Kilimanjaro Mountain 241
Kintampo Rope 234
Kipengere Mountain 241
Lady Burton's Rope 235
Lunda Rope 232
Lushoto Mountain 241
Mutable Sun 226
Ochre Bush 239
Punctate Sun 228
Red Tanganyika Mountain 240
Red-bellied Bush 242
Red-cheeked Rope 233
Red-legged Sun 227
Ribboned Rope 232
Rwenzori Sun 225
Slender-tailed 229
Smith's Bush 240
South African Ground 244
Striped Bush 239
Striped Ground 243
Thomas's Rope 233
Unstriped Ground 245
Vincent's Bush 242
Western Palm 230
Zanj Sun 226
squirrels 225
bush 236–237
ground 243
palm 230
rope 231
sun 225
Tanganyika mountain 240
Steatomys 264
Steenbok 549
Stenocephalemys 288
Stenonycteris lanosus 330
Stochomys longicaudatus 295
Strepsirrhini 185–211
Suidae 476–485
Suncus 316
Suni 526
Surdisorex 315
Suricata suricata 445
Sus scrofa 477
Sylvicapra grimmia 532
Sylvisorex 317
Syncerus caffer 503

Tachyoryctes 259
Tadarida 346
Talapoin, Northern 145
Southern 146
Taphozous 344
Tatera see *Gerbilliscus*
Tateril 275
Taterillus 275
Taurotragus derbianus 518
Taurotragus oryx 519
Tenrecidae 69–70
Thallomys 297
Thamnomys 294
Theropithecus 127
Theropithecus gelada 127
Thryonomyidae 219–220
Thryonomys gregorianus 219
Thryonomys swinderianus 220
Tiang 596
Topi 596
Tragelaphini 505–506
Tragelaphus angasi 508
Tragelaphus buxtoni 510
Tragelaphus eurycerus 517
Tragelaphus imberbis 507
Tragelaphus scriptus 513
Tragelaphus spekii 515
Tragelaphus strepsiceros 511
Tragulidae 490–491
Triaenops afer 342
Trichechidae 66–68
Trichechus senegalensis 67
Tsessebe 596
Tubulidentata 86–88

ungulates, even-toed 475
horned 500–502
odd-toed 461
Uranomys ruddi 271
Uromanis tetradactyla 456

Vespertilionidae 351–359
Viverridae 408–421
Vole, Mediterranean 267
Vulpes cana 373
Vulpes chama 374
Vulpes pallida 375
Vulpes rueppelli 375
Vulpes vulpes 376
Vulpes zerda 373

Walo 279
Warthog, Common 484
Desert 483
warthogs 482
Waterbuck 586
Common 586
Defassa 586
Weasel, African Striped 382
Common 380
Libyan Striped 381
Whippomorpha 486–490
Wildcat 405
Wolf, Ethiopian 369
Grey 371

Xenogale naso 432
Xerus 243
Xerus getulus 245
Xerus erythropus 243
Xerus inauris 244
Xerus princeps 243
Xerus rutilus 245

Zebra, Common 465
Grevy's 463
Mountain 467
Zelotomys 287
Zenkerella insignis 255
Zorilla 381